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THE DISTRIBUTION OF NERVES IN THE UPPER LIMB, WITH REFERENCE TO VARIABILITIES AND THEIR CLINICAL SIGNIFICANCE[1]

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1. INTRODUCTION.

This investigation was undertaken with the following objects:

(1) To assist the clinician, by means of measurements, as to the position of origin of important branches of the nerves of the arm and as to the limits within which he may expect to find variations of these branches;

(2) to give average positions for the entry of muscular nerves into their respective muscles, and also the variabilities to be expected;

(3) to determine the positions at which the larger sensory branches become cutaneous;

(4) to study, as far as dissecting-room subjects will permit, the communications taking place between cutaneous nerves;

(5) to point out any anatomical anomalies and variabilities found in the nerve supply of the upper limb which may be of significance in helping to elucidate various problems presented clinically by soldiers wounded during the war. Clinical investigation and the surgical treatment of the very numerous cases of peripheral nerve injury has shown that a more precise knowledge than is to be found in the standard anatomical textbooks was required about the above points.

For this reason 26 adult and eight foetal limbs have been examined. The method employed has been to take measurements accurate to ·5 cm. between convenient bony points of the limbs examined. The bony points used were the tip of the acromion process and the tip of the external condyle of the humerus for upper arm measurements, and the tip of the external condyle and the tip of the styloid process of the radius for measurements in the forearm, the limb being always adducted to the side with the forearm supinated. The level at which the branch of the nerve under examination arose from its parent trunk, entered a muscle, became cutaneous, etc., was marked off on a vertical scale stretching between the two bony points used. For example, if the distance in an upper arm was found to be 30·0 cms. between the tip of the acromion process and the tip of the external condyle of the humerus and the branch of the musculo-cutaneous to the biceps was found to enter this muscle at the

[1] This thesis was submitted for the degree of M.D. at Manchester in May 1920, and was awarded commendation.

level of 15·5 cms. along this scale, that measurement was noted under that limb as $\frac{15{\cdot}5}{30{\cdot}0}$. This fraction expressed as a decimal or ratio is ·52. From a series of such ratios obtained by the measurement of numerous limbs an average ratio can be obtained, as shown in column 3 of the Tables in section 11. This average ratio is a constant for all limbs. The average length of the upper arm is found to be 30·5 cms. and so the application of this figure to the constant, or average ratio, gives an average distance in centimetres for the entry of the nerve to the biceps in an upper arm of average length. In correcting the distance for any particular arm under examination, e.g. for one 33·5 cms. long, all that is required is an application of the constant to this figure, ·52 × 33·5. This, within slight limits of variability to be described later, will give a definite position at which the clinician may confidently expect to find the branch of the musculo-cutaneous nerve entering the biceps.

It is to be carefully noted that all measurements refer to horizontal *levels* and bear no relation to the actual length of the nerve unless, between two measurements, the nerve happens to pass vertically down the limb and in one vertical plane.

The dissections of foetal limbs have not been included in this series of measurements. The average ratio or constant was found to correspond with that of the adult series, but the great disparity of length between foetal and adult limbs so lowered the average length measurements as seriously to affect the average readings of the positions taken.

The foetal limbs have however been of value, particularly in studying the brachial plexus and the distribution of cutaneous nerves.

The application of this principle to about forty important definite points in the course of the nerves of the upper limb has resulted:

(1) in a series of average measurements from which the course of the various nerves can be accurately mapped out, and

(2) in a series of average ratios or constants (column 3, Tables, section 11) from which the clinician can obtain the above series of average measurements in any limb he is investigating provided he knows the length of that limb.

In the subsequent descriptions the brachial plexus will first be dealt with and then will follow an account of each of its branches of distribution to the limb with the exception of the lesser internal cutaneous, which did not seem to be of sufficient clinical importance to warrant its inclusion.

The gross anatomy of the parts will not be considered except where it is necessary in order to explain any points of interest or anomalous conditions which may require description. Anomalies will be described under the various nerves in the course of which they occur. Variabilities in position of branches of distribution will also be considered under their respective nerves and these variabilities will be given in their corrected form. To explain this the nerve supply to the biceps may be again taken as an example. Let us suppose that

the muscle-entry of this nerve is found to vary between 12·0 and 18·0 cms. in various arms. This may be termed *gross variability* and would be inaccurate as the upper arm giving the first measurement was found to be 28·0 cms. long, and that giving the second 34·0 cms. The ratios in these cases were therefore $\frac{12{\cdot}0}{28{\cdot}0}$ and $\frac{18{\cdot}0}{34{\cdot}0}$ or ·42 and ·53. This therefore reduces the variability to ·11, which, taking the average upper arm as 30·03 cms. in length, is 3·3 cms. The *corrected variability* of this branch would therefore be 3·3 cms.

The figures used in this example are not accurate, but they will serve to explain the principle of these measurements. The subject will be referred to again when the actual figures are considered.

2. BRACHIAL PLEXUS

The gross anatomy of the formation of the trunks and cords of the brachial plexus has been found to correspond so accurately with the description in the textbooks that it need not be mentioned here.

The branches of the brachial plexus are generally divided into a supraclavicular and an infraclavicular set. This is indefinite and inaccurate, and is consequently of little clinical value. To substantiate this statement the position of origin of the external and internal anterior thoracic nerves has been observed with some care. These branches are described as infraclavicular in origin. In the fully abducted position of the limb, when the outer end of the clavicle is considerably raised with reference to its level in the orthodox "anatomical position," the external anterior thoracic is found to arise distinctly above the clavicle and the internal anterior thoracic has at least a postclavicular if not a supraclavicular origin. In the anatomical position, therefore, with the arm adducted to the side, these branches must be even more supraclavicular in origin due to the dropping of the outer end of the clavicle. In view of this inaccuracy and of the lack of definition in using the clavicle as a line of subdivision on account of the considerable excursion of this bone with motion of the limb, it has seemed advisable to look for some definite line by which may be effected a subdivision which is not dependent on the vagaries of the moving clavicle (1).

In the fully abducted position of the limb, the trunks, cords and their terminal divisions, may be described as passing horizontally from the root of the neck into the limb. It is found that the point of junction of the three posterior divisions of the trunks to form the posterior cord is constant. If now a vertical line be drawn through the plexus cutting this point, a definite line of division of the plexus is obtained which is constant for all limbs, showing only very slight variations proportionate with the dimensions of the individual subject. A series of measurements of 21 limbs has established this line as being on an average 7·75 cms. from the lateral border of the lower cervical vertebral bodies (fig. 1). In the living, the pulsations of the common carotid artery will form a better landmark and 6·75 cms. horizontally outwards from the

lateral border of the common carotid at the root of the neck will give the same line of division. This line, where it cuts the plexus, is definitely distal to the clavicle.

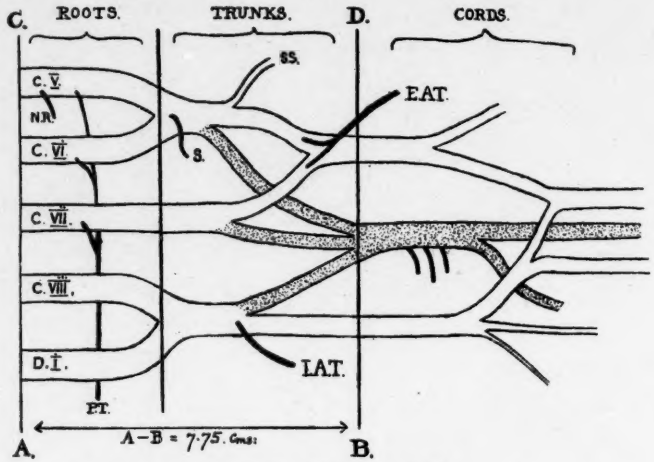

Fig. 1. Brachial plexus (left).

C.A. = line of lateral borders of bodies of lower cervical vertebrae.
D.B. = subdivisional line separating trunks from cords.
S.S. = suprascapular nerve.
S. = nerve to subclavius.
N.R = nerve to rhomboids.
P.T. = posterior thoracic nerve.
E.A.T. = external anterior thoracic nerve.
I.A.T. = internal anterior thoracic nerve.

The use of this line should simplify the nomenclature of the branches of the plexus, besides eliminating the clavicle from consideration in this respect. The branches would be classified as

(*a*) branches of the roots,
(*b*) branches of the trunks,
(*c*) branches of the cords.

The line would divide the trunks from the cords. The branches of the roots would remain as before, as would those of the cords. The trunk branches as at present described are two, the suprascapular and nerve to the subclavius, both from the upper trunk. To these would have to be added the two anterior thoracic nerves and such an addition appears to be justifiable. An examination of the origins of these nerves in 25 subjects (including foetuses) shows the following points.

Internal anterior thoracic nerve. This nerve arises from the plexus at a higher level than is compatible with its origin from the inner cord. Gray (2) recognises this high origin by describing it as a posterior relation of the first

part of the axillary artery, which portion of the vessel is always considered as an inferior relation of the three trunks of the plexus. The actual origin of the nerve is occasionally directly from the anterior aspect of the lower trunk. Generally, however, it arises from the anterior aspect of the trunk immediately distal to the origin of its posterior division which is going to assist in the formation of the posterior cord. It is customary to say that the lower trunk divides into an anterior and posterior division but the anterior division is not considered as a separate entity, in other words the inner cord is described as beginning immediately the posterior division of the lower trunk has arisen. It would seem better to give the anterior division of the lower trunk a definite length and to consider it as extending downwards to the dividing line described (*BD*, fig. 1), distal to which line it could justifiably be called the inner cord. The internal anterior thoracic nerve does therefore belong definitely to the trunk branches and should be considered as arising from the anterior division of the lower trunk.

External anterior thoracic nerve. This should also be considered as a branch of the brachial nerve trunks. Observations on the origin of this nerve have been taken in a series of 21 adult and four foetal limbs. The nerve has been found to arise either by two separate roots from the anterior divisions of the upper and middle trunks, or by a single root placed exactly at the angle where these two anterior divisions join to form the outer cord. In 60 per cent. the origin was by two roots from the anterior divisions of the trunks, and in the remainder the single root origin so obviously came from these two divisions, immediately after their union, that only technically could the nerve be considered as a branch of the outer cord.

When the anterior divisions of the upper and middle trunks join they are classically considered as forming the outer cord immediately. If, now, we consider this cord as being formed at the level of the dividing line, *BD* in fig. 1 as suggested, the external anterior thoracic will, in any case, be included as a trunk branch and will be rightly described as arising from the anterior divisions of the upper and middle trunks.

The anterior thoracic nerves should therefore be considered, from both anatomical and clinical points of view, as branches of the brachial nerve trunks, and not as branches of the outer and inner cords as usually described. The dividing line here suggested will place them both in this category.

Passing now to the segmental constitution of the cords, a variability has been observed which has not been sufficiently emphasised in English text-books, but which is of very considerable clinical significance.

The inner cord is generally described as drawing its fibres solely from the eighth cervical and first dorsal roots. In a very considerable proportion of cases the seventh cervical root also gives fibres to the inner cord in the following manner:

The outer head of the median contains fibres from the sixth and seventh cervical roots. This nerve bundle joins the inner head of the median to form the median trunk.

Frequently, however, a considerable bundle of fibres from the inner aspect of the outer head of the median becomes separated off immediately above the formation of the median trunk. This bundle, consisting of seventh cervical fibres, runs obliquely downwards and inwards behind the inner head of the median to enter the ulnar nerve. Hence the ulnar nerve frequently contains fibres from the seventh cervical root in addition to its eighth cervical and first dorsal fibres (fig. 2). The significance of this distribution of fibres will be discussed when dealing with the ulnar nerve.

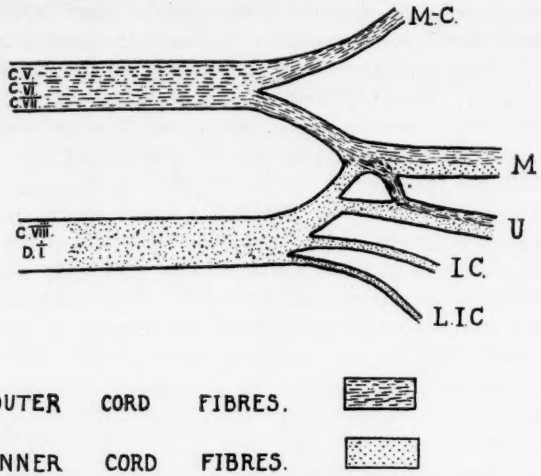

Fig. 2. Communication between outer and inner cords. Right brachial plexus (from behind).
M.C. = musculo-cutaneous nerve.
M. = median nerve.
U. = ulnar nerve.
I.C. = internal cutaneous nerve.
L.I.C. = lesser internal cutaneous nerve.

This interchange of fibres between the outer and inner cords has been looked for in 21 foetal and adult subjects and has been found to be present in 57 per cent.

Wilfred Harris (3) in his paper on the true form of the brachial plexus gives a positive result in 86 per cent. of the 30 subjects examined. He includes in this percentage a number of cases in which, by careful dissection of excised brachial plexuses removed at postmortems, he was able to trace a bundle of fibres down the outer head of the median, up its inner head and thence down again into the ulnar nerve.

Whatever the exact percentage may be, my estimate of 57 per cent., in which the condition was quite obvious without minute dissection, may be taken as a minimum. This variability is consequently well worthy of emphasis in textbooks, especially in view of its clinical significance in helping to explain variabilities in the cutaneous distribution of the ulnar nerve.

3. MUSCULO-CUTANEOUS NERVE

Origin. This nerve shows considerable variability in its origin from the outer cord.

In four out of the 26 cases the outer cord did not split into two divisions and the muscular branches of the musculo-cutaneous arose direct from the lateral aspect of the outer cord. The cutaneous division of the nerve was separated from the cord about the junction of the middle and lower thirds of the arm, from which point it proceeded downwards and outwards between the biceps and brachialis anticus to its normal distribution. This anomalous origin of muscular branches did not affect the average level at which the coraco-brachialis, biceps and brachialis anticus are normally supplied.

Another anomaly occasionally found in this region was a musculo-cutaneous trunk containing fibres destined to join the median. These fibres were given off in a bundle to join the median trunk at a variable distance down the upper arm. The size of this anomalous nerve bundle, which has been noted by several other workers, varies inversely with the size of the outer head of the median, and this bundle appears to consist merely of a variable number of "median" fibres which have descended for a short distance in the trunk of the musculo-cutaneous nerve.

Distribution. In describing the distribution of the nerves the numbers given will refer to horizontal levels down the average upper arm or average forearm.

The average upper arm is found to measure 30·5 cms. from the tip of the acromion process to the tip of the external condyle of the humerus. The average forearm, measured from the latter bony point to the tip of the styloid process of the radius, is 24·04 cms. long. These two numbers should, therefore, be borne in mind throughout the subsequent description of the individual nerves.

I. Muscular distribution

In such an average upper arm (30·5 cms.) the levels at which muscular branches arise from the musculo-cutaneous nerve trunk and enter their respective muscles will be shown by the following figures:

Nerve to coraco-brachialis	arises	4·76 cms.	(·156)
„ „	enters	7·35 „	(·241)
Nerve to biceps	arises	12·99 „	(·426)
„	enters	15·28 „	(·501)
Nerve to brachialis anticus	arises	17·32 „	(·568)
„ „	enters	20·27 „	(·665)

Nerve to coraco-brachialis. A slender bundle of fibres arising from the lateral aspect of the nerve trunk high up in the upper arm. After a course of about 2·5 cms. it ends by entering the medial aspect of the muscle just above the point at which the coraco-brachialis is pierced by the main musculo-cutaneous trunk.

Nerve to biceps. A stout branch arising from the nerve trunk as this is proceeding obliquely distally and laterally between biceps and brachialis anticus. After a short course distally and forward it divides into two branches, one entering the deep surface of each belly of the muscle at the same horizontal level. The above figures bring out two points. First, the nerve to the biceps is very short and secondly it enters the muscle immediately below the middle of the brachium $\left(\frac{15{\cdot}28}{30{\cdot}50}\right)$.

Nerve to brachialis anticus. This nerve arises from the inferior aspect of the main trunk while it is lying between biceps and brachialis anticus. Its extra-muscular course is longer than that of the nerve to the biceps and it ends by breaking up into four or five large branches which penetrate the anterior aspect of the muscle over a considerable area. From the measurements it will be observed that this branch arises only about 2 cms. below the middle of the upper arm and that it enters the muscle approximately at the junction of the middle and lower thirds of the brachium.

From these points it follows (i) that a lesion of the musculo-cutaneous trunk below 17·32 cms. of the upper arm will result in an anaesthesia of the musculo-cutaneous area uncomplicated by any muscular paralysis, and (ii) that however extensive any lesion of the upper arm may be, provided its upper limit is distal to 20·27 cms., the branch to the brachialis anticus will be uninjured and consequently a simple sensory lesion will again be the result in so far as the musculo-cutaneous nerve is concerned.

II. Cutaneous distribution

It will be noticed that the musculo-cutaneous gives off its last motor fibres higher up in the arm than is generally realised, 17·32 cms. This is of interest in view of the fact that a lesion of the musculo-cutaneous trunk a very short distance below the middle of the brachium will result in an uncomplicated sensory lesion. Stopford states that an uncomplicated sensory lesion of this nerve is five times as common as a mixed lesion.

Of the two cutaneous divisions of this nerve the anterior is the larger. The posterior division seldom reaches to the wrist, generally ending on the back of the lower part of the forearm. Occasionally this division ends by anastomosing with the lower external cutaneous branch of the musculo-spiral (fig. 4).

The anterior division can always be traced beyond the wrist and terminates by supplying a variable portion of skin over the thenar eminence. This division is in close relation with the radial nerve, which is becoming cutaneous in the lower part of the forearm by appearing behind the supinator longus tendon. In this region, therefore, there is frequently a communication between the musculo-cutaneous and radial nerves, which is a matter of clinical importance as probably explaining the slightness or absence of sensory disturbance in cases of section of the radial nerve above the lower third of the forearm (4). An

attempt has consequently been made to find how often this anastomosis occurs, but there have been obvious difficulties in studying limbs dissected by students who do not reverence cutaneous nerves. In only seven limbs was it possible to be certain whether or not this anastomosis occurred, and these seven gave five positive results. In the other two no trace of a communication could be found, although the dissection was carefully performed. Two of these anastomoses are shown in figs. 3 and 4. It will be seen from these figures

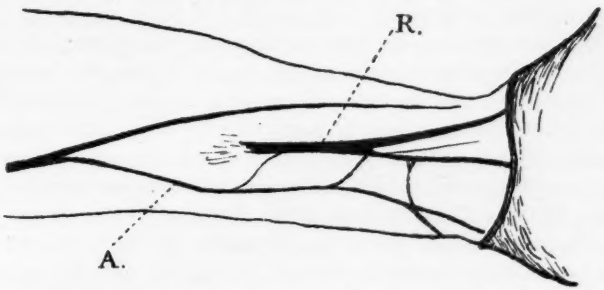

Fig. 3. Communication between musculo-cutaneous and radial nerves.
R = radial nerve.
A = anterior division of musculo-cutaneous nerve.

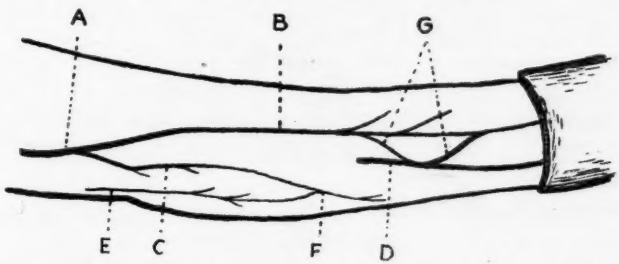

Fig. 4. Communications between musculo-cutaneous, musculo spiral and radial nerves.
A = musculo-cutaneous nerve trunk.
B = anterior division of musculo-cutaneous.
C = posterior division of musculo-cutaneous.
D = radial nerve.
E = lower ext. cut. branch of musculo-spiral.
F = communication between lower ext. cut. branch of musculo-spiral and post. div. of musculo-cutaneous.
G = communication between ant. div. of musculo-cutaneous and radial nerves.

that the size and complexity of the anastomosis vary greatly. In fig. 3 two large bundles of fibres are seen entering the radial nerve, whereas in fig. 4 the anastomosis consists only of two small filaments and the latter is the condition more frequently met with.

An attempt to find this communication in foetuses was unsuccessful, the filaments being too minute to trace with any accuracy in these small limbs.

The interchanged fibres become inextricably bound up with the radial nerve and are presumably distributed in the branches of the latter.

It is of some clinical importance to remember that this communication may not be present.

4. MEDIAN NERVE

The median trunk is normally formed to the lateral side of the proximal part of the brachial artery by the union of its outer and inner heads, the outer head being slightly the larger.

This origin is subject to some variation. The fibres composing the inner head are constant, but those forming the outer head may be partially, or completely, carried down in the musculo-cutaneous trunk to be given off from that trunk to the inner head, and thus form the median nerve, at variable distances down the upper arm. This low origin was found in three of my cases. In one of these the nerve was only formed at the junction of the fourth and lowest fifth of the upper arm. Occasionally only some of the fibres of the outer head join the inner head in the normal position, the remainder joining it, *via* the musculo-cutaneous trunk, at a lower level. On both sides of one body the median nerve passed deep to the brachial artery to get from its lateral to its medial side.

Distribution

Muscular. The multiple muscular branches of the median immediately distal to the elbow show such tremendous variability and come off so close together that estimations of their average levels must be only approximate. The nerve to the pronator radii teres can be distinguished as a separate branch but the supplies of flexor carpi radialis, palmaris longus and flexor sublimis digitorum have been classed as one nerve bundle. In the average forearm 24·04 cms. long the

Nerve to pronator radii teres arises 1·0–2·0 cms. approx.
„ „ enters 1·5–2·0 „ approx.
Nerve bundle to the common flexor mass, upper limit of origin = 2·08 cms. (·086)
„ „ upper limit of entry = 2·76 „ (·115)
„ „ lower limit of entry = 5·05 „ (·210)
Anterior interosseous nerve arises 5·24 cms. (·218)

Nerve to pronator radii teres. This is the first branch of distribution of the median. Although its origin may be given as approximately 1·0–2·0 cms. below the tip of the external condyle this point varies greatly in both directions. As a general rule it arises below the external condyle, but it has been found coming from the trunk as much as 4 cms. above this bony point. Its direction is medially and slightly distally. As it approaches the muscle it commonly divides into an anterior and a posterior branch, the anterior entering the lateral aspect of the condylar head of the muscle and the posterior supplying the coronoid head at its origin from the ulna. The level of the entry to the muscle is approximately from 1·5–2·0 cms., therefore its direction is practically

horizontal, the posterior branch descending a little to gain the coronoid head. Occasionally the nerve to the coronoid head of the muscle arises by a separate branch just below that for the condylar head, and in one case such a branch entered the coronoid head as low as 6·0 cms. down the forearm. It is therefore anatomically possible to have paralysis of either of the heads of the muscle alone in lesions of the anterior or posterior branches when these arise from a common trunk. When these branches arise independently, section of the median between their points of origin will paralyse the coronoid head leaving the condylar head intact. It is doubtful whether this point is of clinical value as the coronoid head of pronator radii teres is generally very small and its reactions cannot be tested clinically apart from those of the condylar head.

Frequently the nerve supply to the condylar head arises by two distinct roots.

Bundle to the common flexor mass. A large bundle of fibres arising from the antero-medial aspect of the nerve trunk at about 2·0 cms. down the forearm. This bundle proceeds forwards and medially towards the muscles it supplies, expanding as it goes into a triangular sheet of fibres. The highest fibres are directed medially and a little distally to reach the flexor carpi radialis. The lower fibres descend more and more obliquely to reach the palmaris longus and flexor sublimis digitorum. The expanded base of this triangular sheet of fibres is formed where they enter the muscles, the upper limit of entry being 2·75 cms. and corresponding to their entry into flexor carpi radialis and the lower limit, or point of entry into palmaris longus and flexor sublimis digitorum being a little more than 5 cms. down the forearm. The base of this triangle has therefore a vertical length of nearly an inch. In accordance with this increasing obliquity of nerve fibres a lesion involving the supply to the flexor sublimis digitorum is more likely to injure the median trunk than is damage to the nerve to flexor carpi radialis.

The flexor sublimis digitorum does not, however, receive all its nerve fibres in this situation. In 11 cases out of this series of 24 I was able to find a branch of the median mentioned by Quain (5), which arises in the lower part of the forearm, while the nerve is lying between the superficial and deep flexor muscles, and which proceeds practically horizontally forwards with a slight inclination distally to end in the posterior aspect of the index or occasionally of the medius belly, of the flexor sublimis digitorum. The level at which this branch arises is not sufficiently constant to give anything of a reliable average measurement. Its height of origin in my cases varies between 9·0 cms. and 22·5 cms. down the forearm, but in the majority of cases it was below 12·0 cms. It entered the muscle belly, on an average, 1·0 cm. below its origin. The paralysis of this branch may help to explain weakness of flexion confined to the index finger in median injuries in the second quarter of the forearm.

Clinically this branch seems to have been very constant. Professor Stopford tells me that in all of nine patients in whom complete division of the median in the middle of the forearm was verified at operation, the belly of the flexor

sublimis digitorum to the index finger was paralysed. This nerve may, then, be the sole supply of the index belly of the muscle.

Anterior interosseous nerve. This is the next distinct branch of the median. It arises 5·24 cms. down the forearm and proceeds distally and dorsally to reach the interosseous membrane and lie between the flexor profundus digitorum and flexor longus pollicis. Just before it reaches the interosseous membrane it gives a branch from its medial side to the lateral portion of the flexor profundus digitorum and, at about the same level, one from its lateral side, which enters the upper extremity of the flexor longus pollicis. In the proximal part of its course on the interosseous membrane it supplies a few additional twigs to the upper ends of these muscles and then, greatly reduced in size, runs vertically downwards. At the junction of the third and lowest quarters of the forearm it disappears under the pronator quadratus, which muscle it supplies on its deep aspect.

This completes the muscular distribution of the median in the forearm, as the branch to the index belly of the flexor sublimis digitorum has been described in connection with that muscle.

Muscular distribution in hand

The median nerve is classically described as supplying abductor pollicis, opponens pollicis and the superficial head of flexor brevis pollicis. It has been found clinically, however, that the superficial head of flexor brevis pollicis may react well to faradic stimulation in cases of median paralysis, although the abductor and opponens pollicis do not respond. The difficulty, as Wood-Jones (6) points out, appears to be principally one of nomenclature, and the problem resolves itself into the answer to the question "What exactly is the superficial head of flexor brevis pollicis?" If the answer to this question is "That portion of flexor brevis pollicis which obtains insertion to the radial sesamoid and to the radial side of the base of the proximal phalanx of the thumb" an electrical response will be obtained from this "superficial head." Wood-Jones shows that this slip of muscle attached to the radial side of the first phalanx of the thumb is divisible into a superficial and deep portion. The superficial portion, which arises practically entirely from the anterior annular ligament, is supplied by the median nerve. The deeper portion gets its nerve supply from the ulnar and it is this portion of the "superficial head" of flexor brevis pollicis which reacts to stimulation when the median nerve is paralysed.

Cutaneous distribution

Palmar cutaneous. A minute twig arising a variable, and generally considerable, distance proximal to the wrist-joint. It runs down on the anterior surface of the main trunk to appear at the wrist-joint between palmaris longus and flexor carpi radialis. Then, running over the anterior annular ligament, it terminates by supplying a small area of skin over the middle of the proximal part of the palm.

Cutaneous supply to fingers. This supply varies inversely with variations in the palmar digital distribution of the ulnar nerve, and to save re-duplication of description the nerve supply of the fingers will be discussed when dealing with the ulnar nerve.

5. CIRCUMFLEX NERVE

This branch of the brachial plexus arises from the posterior cord as this is lying on the subscapularis muscle. The nerve runs distally to the lower border of this muscle when it turns backwards through the quadrilateral space. In this situation it is a somewhat intimate relation of the inferior aspect of the capsule of the shoulder-joint and it gives an articular branch upwards to penetrate this aspect of the capsule. Immediately behind the quadrilateral space it ends by dividing into an anterior and posterior division. The level of this division is 6·98 cms. down the arm.

The *anterior division* runs horizontally round the surgical neck of the humerus in contact with the deep aspect of the deltoid muscle. It is exhausted in supplying numerous short twigs of supply to this muscle and ends just short of its anterior border. The terminal twigs described as perforating the muscle to have a cutaneous distribution were not seen.

The *posterior division.* This division takes up a definitely lower level than the anterior one. It gives off, close to its origin, a short stout branch which proceeds upwards and medially to sink into the teres minor muscle. The remaining fibres then wind round the posterior border of the deltoid muscle and immediately pierce the deep fascia to become cutaneous. This division takes a horizontal course on the superficial surface of the deltoid similar to, but at a somewhat lower level than, that of the anterior division on its deep surface. By means of ascending and descending branches it supplies the skin over the distal half or more of the deltoid and cannot be traced further forwards than the anterior border of this muscle.

6. ULNAR NERVE

The ulnar is the lowest nerve-trunk split off from the medial aspect of the inner cord of the brachial plexus. It is constant in its level of origin in front of the teres major muscle, lying immediately medial to the termination of the axillary artery and separating this structure from its accompanying venae comites.

In describing the brachial plexus it has been observed that the ulnar nerve obtains fibres from the seventh cervical root, in at least 57 per cent. of cases, by means of a communication established between it and the outer head of the median nerve.

The course of the ulnar follows very constantly the accepted description in the textbooks. It leaves the brachial artery at the middle of the brachium by dipping backwards into the posterior muscular compartment. Here it runs distally in contact with the posterior aspect of the internal inter-muscular

septum to the interval between the olecranon and internal condyle of the humerus. Entering the forearm between the two heads of flexor carpi ulnaris it comes to lie on the flexor profundus digitorum, and this deep relation it maintains to the wrist-joint. Passing superficial to the anterior annular ligament the nerve ends at the lower border of this ligament under cover of palmaris brevis muscle by dividing into a superficial and a deep division.

The ulnar has no branches of distribution until it arrives in the region of the elbow-joint. In one case a communicating filament from the internal cutaneous nerve trunk was observed to join the ulnar about the middle of the arm. The first branch of distribution of the ulnar is an *articular branch* to the posterior aspect of the elbow-joint. This is a twig of considerable size, variable in its origin, but seldom coming off higher than 1 cm. proximal to the tip of the external condyle. In one anomalous case this nerve arose as high as the junction of the middle and lower thirds of the arm, and ran distally along with the main trunk for a length of about 12 cms. to reach its distribution to the elbow-joint. Generally, however, this nerve was extremely short and ran practically horizontally outwards to its distribution.

The next series of branches of the ulnar trunk are for the supply of the flexor carpi ulnaris and flexor profundus digitorum.

Nerves to flexor carpi ulnaris. There are, as a rule, two distinct nerves to this muscle, but frequently three and occasionally four separate branches may be seen.

I and II. The two primary and almost constant branches arise from the main trunk, one immediately below the other, and just before the ulnar trunk disappears between the two heads of flexor carpi ulnaris. The level of origin of these two branches was, in this series, ·90 cm. and 1·62 cms. distal to the tip of the external condyle. In two cases (which are not included in this average) the levels of origin of the highest muscular branch were 1·0 cm. and ·5 cm. respectively, proximal to the external condyle. It is exceptional, therefore, for any muscular branch to arise from the ulnar above the elbow-joint or, more accurately, above the tip of the external condyle.

These two primary branches run distally. The upper one is the shorter and ends 2·08 cms. down the forearm by piercing the inner aspect of the olecranon head. The lower branch enters the lateral aspect of the condylar head at 2·99 cms. down the forearm. Tabulated, the measurements of these two nerves are as follows:

Nerve to olecranon head arises ...	... ·90 cm.	(·037)
„ „ enters ...	... 2·08 cms.	(·087)
Primary nerve to condylar head arises	1·62 „	(·067)
„ „ enters	2·99 „	(·125)

III. The next branch, which is not constant but is frequently present, may be spoken of as the secondary nerve to the condylar head. The average measurements are:

Secondary nerve to condylar head arises	2·25 cms.	(·093)
„ „ „ enters	4·88 „	(·203)

This secondary nerve will be seen from these figures to arise a little more than ·5 cm. below the primary branch to this head of the muscle. It will also be observed to have a much longer extra-muscular course than either of the preceding branches. It arises from the medial aspect of the ulnar trunk, runs down with this trunk between the two heads of the muscle and then proceeds obliquely distally and medially on the deep surface of the condylar head to enter the anterior surface of this head at its medial border after an extra-muscular course of over an inch (2·63 cms.).

Poirier and Charpy (7) describe this branch as having an extremely long extra-muscular course and state that it enters the muscle in the lower third of the forearm. Nothing comparable with this length of course was found in any of this series.

IV. The fourth nerve to the flexor carpi ulnaris is a short, inconstant twig which arises from the ulnar after it has disappeared between the two heads of the muscle. It runs forward to enter the deep aspect of the muscle at approximately the same level of entry as the secondary branch to the condylar head.

It has seemed of value to describe this nerve supply fully as the books are vague on the subject, and it is one of clinical importance since injuries to the ulnar nerve in the region of the elbow have been encountered so frequently and displacement of the nerve trunk in front of the internal condyle of the humerus is now a fairly common surgical manœuvre, which permits end-to-end suture to be performed, even when a large defect is found. The freeing of the nerve trunk necessary to allow of this anterior displacement can generally be performed without sacrifice of any of the branches to the flexor carpi ulnaris. The articular branch to the elbow-joint has, however, to be cut as a rule.

To summarise: Four distinct branches may be found arising from the ulnar to supply the flexor carpi ulnaris. In their order of origin these are:

(i) Nerve to olecranon head.
(ii) Primary nerve to condylar head.
(iii) Secondary nerve to condylar head.
(iv) Branch entering muscle immediately below the junction of its two heads.

An analysis of 23 limbs showed the following:

2	cases had	4	branches	(i), (ii), (iii) and (iv).
3	„	3	„	(i), (ii) and (iii).
12	„	2	„	(i) and (ii).
6	„	1	branch.	

(i) and (ii). 17 out of 23 subjects, therefore, had these two branches so that this seems to be the usual method of nerve supply to the muscle.

(iii). Five cases showed this additional branch to the condylar head. This branch, although only present in approximately 20 per cent., is of importance for two reasons. First, on account of the length of its extra-muscular course and secondly, because it may, exceptionally, be the only branch to the

condylar head of the muscle. In one case this nerve entered as low as 8·0 cms. down the forearm.

(iv). The fourth branch is obviously exceptional.

The six cases, in which only one branch was found, showed this branch entering at the junction of the two heads. Its filaments were not traced into the muscle.

The last point to notice in connection with this nerve supply is that the ulnar gives off the first three of these nerves between the average horizontal levels of ·9 cm. and 2·25 cms. down the forearm.

Nerve to flexor profundus digitorum. This branch arises high in the forearm, a short distance below the origin of the lowest nerve to the preceding muscle. The following are its average measurements:

Origin 3·07 cms. (·127),
Entry 5·54 cms. (·230).

The nerve arises from the ulnar trunk while this is lying on the upper fibres of flexor profundus digitorum deep to flexor carpi ulnaris. It is a stout bundle of fibres which runs down on the anterior surface of its muscle for nearly an inch before entering it.

The remaining branches of distribution of the ulnar nerve in the forearm are two, both of which are probably entirely sensory in function.

Dorsal cutaneous branch of ulnar. Two measurements have been taken to fix this branch:

(*a*) its position of origin, 17·06 cms. (·709);

(*b*) the level at which it becomes cutaneous by appearing at the mesial border of the flexor carpi ulnaris muscle, 20·95 cms. (·871).

The measurement of the level of origin shows very marked variation (see Tables, section 11). From its average level of 17·06 cms. the nerve runs distally and very obliquely inwards under flexor carpi ulnaris to gain its second fixation point at the medial border of this muscle. Here it becomes cutaneous at an average level of 20·95 cms. down the forearm and this measurement showed little variability. In the average forearm of 24·04 cms. length the dorsal branch of the ulnar may therefore be considered to become cutaneous a little over 3 cms. proximal to the tip of the styloid process of the radius, and this is therefore a measurement of importance for purposes of localisation in connection with injuries in the neighbourhood of the ulnar side of the wrist-joint.

This is a lower level than is usually given in textbooks. Fig. 5 shows this branch winding round the wrist below the styloid process of the ulna. This is anomalous and is therefore not included in these estimates.

The distribution of this nerve to the dorsum of the hand and fingers has been carefully worked out and will be considered later.

Palmar cutaneous branch. This, the last branch of the ulnar trunk, is a slender twig arising in the lower third of the forearm. It runs down on the

anterior aspect of its parent trunk superficial to the annular ligament to be distributed to the skin over the hypothenar eminence.

The ulnar nerve ends at the distal border of the anterior annular ligament under cover of the palmaris brevis muscle, by dividing into a superficial and a deep division.

The *deep division* dips down between abductor minimi digiti and flexor brevis minimi digiti to supply all the intrinsic muscles of the hand, except those which are innervated by the median and have already been considered.

The superficial division. This is a purely sensory nerve supplying branches to the skin of the ulnar half of the palm and then dividing into terminal

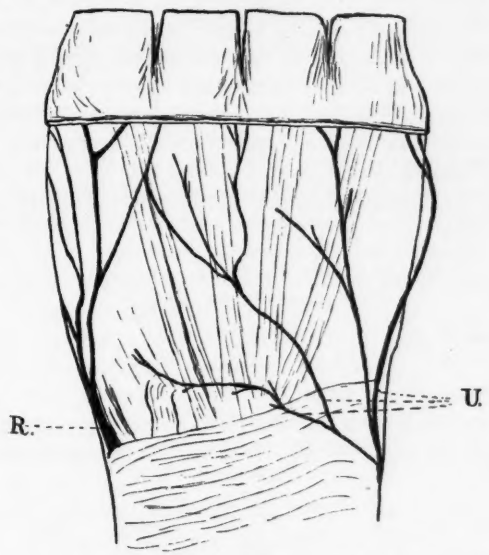

Fig. 5. Dorsal digital distribution of ulnar nerve (Rt).
U. = dorsal cutaneous branch of ulnar nerve.
R. = radial nerve.

branches for the palmar aspect of the ulnar digits. The exact distribution of this nerve will now be considered.

Digital cutaneous distribution of ulnar nerve. The ulnar nerve is usually described as supplying the fifth and the ulnar half of the fourth digit on their palmar and dorsal aspects. Anomalies found clinically have called in question the accuracy of this classical description.

Consequently I have attempted in a series of dissections to arrive at some conclusions as to the variabilities which may be expected to be met with in the cutaneous supply to the fingers.

The ulnar nerve has been taken as the basis in these dissections as, from a complete display of this nerve, it has been considered justifiable to deduce

the digital supply of the median to the palmar aspect and of the radial to the dorsal aspect of the remaining fingers.

In order to supplement observations on dissecting-room subjects a careful dissection of eight foetal ulnar nerves has been performed.

In all, 36 observations have been made—20 on the palmar digital and 16 on the dorsal digital distribution of the nerve.

Palmar digital distribution of ulnar nerve. In the 20 cases of this series, 16 showed the classical supply to the little finger and the ulnar side of the ring finger. Of the remaining four, one supplied the whole of the two ulnar digits and the remaining three had an additional distribution to the ulnar side of the middle finger.

Dorsal digital distribution of ulnar nerve. Of 16 cases, only two showed the classically described distribution to the little finger and the inner half of the ring finger. In eleven cases the distribution was to the little, ring and the ulnar half of the middle fingers. Of the remaining three, one supplied the fingers as far laterally as the ulnar side of the index and two supplied both sides of the two ulnar fingers.

Counting from the ulnar margin of the hand these results may be put in a concise form as follows:

Palmar Digital Distribution

$1\frac{1}{2}$	fingers in	16 cases	= 80 %
$2\frac{1}{2}$	„	3 „	= 15 %
2	„	1 case	= 5 %
		20	100 %

Dorsal Digital Distribution

$1\frac{1}{2}$	fingers in	2 cases	= 12·5 %
2	„	2 „	= 12·5 %
$2\frac{1}{2}$	„	11 „	= 68·75 %
$3\frac{1}{2}$	„	1 case	= 6·25 %
		16	100 %

These figures show, therefore, that, while the palmar digital distribution corresponds with the description in the textbooks, the branches of the dorsal cutaneous branch of the ulnar very frequently supply the whole of the inner two fingers and the ulnar side of the middle finger (fig. 5). Stopford from clinical data comes to the conclusion that "the radial nerve only rarely appears to supply the extensive area of skin usually described, as in about 70 per cent. it does not extend medially beyond the second metacarpal bone (4)."

The dorsal digital branches of the ulnar nerve cannot be traced distally beyond the head of the first phalanx.

In connection with this distribution of the dorsal cutaneous branch of the ulnar it is of interest to remember, as again suggested by Stopford, that the middle is the axial finger of the limb. The seventh cervical is the axial nerve root of the limb. In discussing the brachial plexus the ulnar nerve was found

to obtain fibres from the seventh cervical root by a communication from the outer head of the median in at least 57 per cent. of cases. The dorsal branch of the ulnar supplies the middle finger in 75 per cent. (68·75 per cent. + 6·25 per cent.) of cases. The seventh cervical fibres may be then distributed as a whole, or in part, in this nerve to supply the middle or axial finger.

7. INTERNAL CUTANEOUS NERVE

With the exception of the lesser internal cutaneous this is the highest branch given off from the inner cord of the brachial plexus. It may be considered as arising immediately distal to the lower border of pectoralis minor. It takes up a position on the anterior aspect of the third part of the axillary and the proximal part of the brachial arteries. As a general rule the nerve divides into anterior and posterior divisions in the upper third of the arm.

These divisions run down and pierce the deep fascia close together about the middle of the antero-medial aspect of the arm. Immediately after piercing the fascia the anterior division supplies a constant branch which runs transversely outwards and divides into ascending and descending twigs to supply the skin over the biceps, the descending twigs being traceable as far as the elbow-joint. In two of my cases the internal cutaneous did not divide until it reached the lower third of the arm and, in these, the supply to the skin over the biceps came from the main trunk.

In one case there was a considerable communication between the anterior division and the ulnar in the lower third of the arm.

The anterior division is somewhat larger than the posterior. At the elbow-joint it is an anterior relation to the bicipital fascia and thus to the termination of the brachial artery. It is distributed as low as the lower third of the forearm.

The posterior division diverges from the anterior in the superficial fascia to gain the internal condyle in front of, or occasionally behind, which it proceeds to gain the lateral and posterior aspect of the forearm. It is the smaller of the divisions and can seldom be traced below the middle of the forearm.

The communication described (2) between the internal cutaneous and ulnar nerves at the wrist-joint was never found in this series of cases, and neither of the divisions appeared to get far enough down the forearm to make such an exchange of fibres possible.

As has just been noted a communication may occur between these two nerves in the upper arm and this may be of clinical valuc.

8. MUSCULO-SPIRAL NERVE

This is the largest of the terminal branches of the brachial plexus. It is best considered as a continuation into the arm of the posterior cord of the plexus. The lowest branch of the posterior cord, the circumflex, arises as the cord is lying upon the subscapularis, and the musculo-spiral may therefore

be said to start immediately below this point. From this point of origin, which was found to be very constant, the nerve proceeds vertically downwards in front of the lower fibres of subscapularis, the latissimus dorsi and teres major muscles to leave the axilla and enter the arm, where it is first placed in front of long head of triceps. It now inclines posteriorly and laterally between the long and inner heads of triceps to gain the musculo-spiral groove. Here it lies directly in contact with the bone and is covered by the outer head of the triceps and a fibrous arch thrown over the groove from the deep aponeurosis of this head. The musculo-spiral groove conducts the nerve obliquely distally and laterally to the external inter-muscular septum, which it pierces at the junction of the middle and lower thirds of the arm to appear between the supinator longus and brachialis anticus muscles. A vertical course thence, deeply between the supinator longus and extensor carpi radialis longior on its outer and the brachialis anticus on its inner side, carries it to its termination, which shows very considerable variation. In 23 measurements the variability of termination of this nerve was from 4·5 cms. above to 4·0 cms. below the tip of the external condyle. In nine cases it was above this point and in eleven below it. In the remaining three the nerve split into its two terminal divisions immediately in front of the tip of the external condyle.

This bony landmark therefore gives a good average position of termination of this nerve(2), but it should be remembered that it has a variability of approximately 4 cms. above and below this point.

Distribution

Muscular. Up to the point where the musculo-spiral pierces the external inter-muscular septum, i.e. in the upper two-thirds of the arm, the muscular branches of distribution are those to the triceps and anconeous muscles.

Nerve supply of triceps (fig. 6). The triceps is supplied by four distinct bundles of nerve fibres from the musculo-spiral and their average positions will be seen from the following table:

I.	Nerve to long head arises	7·11 cms.	(·233)
	„ „ enters	11·30 „	(·370)
II.	Ulnar collateral arises	9·53 „	(·312)
	„ „ enters	18·17 „	(·595)
III.	Nerve to outer head arises	10·13 „	(·332)
	„ „ enters	14·62 „	(·479)
IV.	Nerve to inner head arises	11·21 „	(·368)
	„ „ enters	18·26 „	(·599)

There is one general point about the branches of the musculo-spiral which will be most conveniently referred to here. The nerve bundles are arranged and receive their individual sheaths of perineurium a considerable distance above the point where they are given off as branches. These branches are bound to the main trunk merely by the epineurium and are consequently easily split up from the nerve to some distance above their normal point of origin. This discretion of nerve bundles in the main trunk was observed to some extent

in all the nerves but it is so marked in the case of the musculo-spiral as to deserve special mention. The dissection was carried out to avoid this splitting up as far as possible, as the object of these measurements is to show where the nerve actually leaves the main trunk, but its recognition is of practical importance particularly

(1) in the operation of fascicular suture,

(2) in explaining certain dissociated paralyses.

Fig. 6. Nerve supply of Triceps
A = long head of Triceps.
B = outer head of Triceps.
C = inner head of Triceps.

Nerve to the long head of triceps. This bundle of fibres is the first branch of the musculo-spiral. It arises while the main trunk is still in contact with the posterior axillary wall at 7·11 cms. After a course of over 4 cms. distally and medially it ends by piercing the anterior surface and lateral border of the long head of the muscle at 11·3 cms. A point to emphasise is the height of its origin. The internal cutaneous branch of the musculo-spiral generally arises in common with this muscular bundle. The bundle splits into numerous branches some

distance before it gains the muscle and these terminal branches enter the long head over a considerable area, the highest at least a centimetre above the lowest. The figure of entry, 11·3 cms., is a mean measurement.

Ulnar collateral nerve. This branch arises at 9·53 cms., which corresponds approximately to the lower border of teres major. It is the inner and smaller nerve to the inner head of the triceps. It has a long extra-muscular course distally and slightly medially, first resting on the ulnar nerve and then on the internal inter-muscular septum which it pierces about 18·0 cms. down the arm to sink immediately into the inner head of triceps. It has the longest extra-muscular course of any of the branches to the triceps. This nerve is therefore sometimes injured in lesions of the ulnar nerve, but it has not been found clinically to be of importance as a nerve supply of this head of triceps (Stopford).

Nerve to the outer head of triceps. A bundle of fibres arising about half a centimetre below the ulnar collateral and the last of the branches coming off definitely on the medial side of the arm. Its general direction is laterally with an inclination distally. As it approaches the muscle it divides into numerous subdivisions which enter the medial aspect of the outer head of the muscle over an area with a vertical depth of half to one centimetre. The mean level of its entry is 14·62 cms.

Frequently this nerve arises by a large common trunk, which includes the nerve to the inner head of triceps and the lower external cutaneous branch of the musculo-spiral.

Nerve to the inner head of triceps. This is a branch of considerable size arising just as the main trunk is entering the musculo-spiral groove at an average level of 11·21 cms. It proceeds distally and very slightly laterally and, after an extra-muscular course of 7·0 cms., it enters the fibres of the inner head of the triceps. The terminal filaments of this nerve run through the triceps to supply the greater part of the anconeous muscle. This nerve is definitely larger than the ulnar collateral so that, although a few of its fibres end in the anconeous, it is probably the more important nerve of supply to the inner head of triceps. This observation seems to get confirmation from clinical evidence of lesions of the ulnar collateral nerve.

As previously mentioned this bundle of fibres sometimes arises by a common trunk with the fibres destined for the outer head of the muscle and, more frequently, with those which eventually go to form the lower external cutaneous branch.

In connection with the nerve supply of the triceps there are certain points of special significance. The musculo-spiral is most vulnerable while it lies in the musculo-spiral groove. The musculo-spiral groove corresponds in vertical length with the middle third of the upper arm. All the nerves to the triceps except the nerve to the inner head arise in the upper third of the arm, i.e. above the musculo-spiral groove. The nerve to the inner head arises just at the upper limit of the groove. No other muscular branches arise while the main trunk is in the groove. Consequently (i) an uncomplicated lesion of the trunk in the

musculo-spiral groove is very unlikely to affect the nerve supply of the triceps, and (ii) when the surgeon is operating on the musculo-spiral in the groove there are no important muscular branches for him to look for and establish the integrity of. The only important branch which generally arises definitely in the groove is the lower external cutaneous. A piece of clinical evidence confirming these anatomical facts is found in the statement that in 25 cases of injury to the musculo-spiral in the middle third of the brachium, in which complete division of the main musculo-spiral trunk was proved at operation, there was no paralysis of any head of triceps (Stopford).

The remaining muscular branches arise well within the lower third of the upper arm after the trunk has pierced the external inter-muscular septum. They are distributed to brachialis anticus, supinator longus and extensor carpi radialis longior in that order proximo-distally.

Nerve to the brachialis anticus. This branch is by no means constant. When present it arises about 24·0 cms. down the upper arm. It has a very short course running transversely inwards, sometimes with an inclination upwards, to enter the superficial aspect and lateral border of the muscle. Electrical stimulation of this branch on the operating table has shown no effect on the muscle, from which it is considered probable that this nerve is an afferent nerve-path (H. Platt).

Nerve to the supinator longus.

Arises 25·23 cms. (·827).
Enters 28·26 „ (·927).

This branch arises from the anterior aspect of the musculo-spiral and, after proceeding vertical downwards for about 3 cms., terminates in the inner surface of its muscle. This branch is frequently duplicated. In two of my cases it entered the muscle as low as the tip of the external condyle (30·5).

Nerve to the extensor carpi radialis longior. This nerve was extremely constant in its origin at an average of 26·79 cms. down the arm, roughly 1½ cms. below the origin of the nerve to supinator longus. It proceeds distally and slightly laterally, somewhat deep to the preceding nerve, to enter the medial border of its muscle. As an average level of entry into its muscle a point should be taken immediately above the tip of the external condyle. In 22 measurements the nerve entered the muscle, in the upper arm in 11, in the forearm in seven and directly opposite the tip of the external condyle in four cases. The highest level of entry noted was 2 cms. above, and the lowest, 2·5 cms. below the condyle. These figures exclude an anomalous case in which the nerve arose from the posterior interosseous trunk and entered the muscle as low as 5·5 cms. below the external condyle.

Cutaneous. Three cutaneous nerves are generally described as arising from the musculo-spiral trunk:

(i) Internal cutaneous.
(ii) Upper external cutaneous.
(iii) Lower external cutaneous.

Internal cutaneous. This branch arises in the axilla, generally from one of the muscular branches to the long head of triceps (7·11 cms.). After effecting communications with the intercosto-humeral nerve and the lesser internal cutaneous it winds round the medial border of the long head of triceps to gain the back of the brachium. It runs vertically downwards in the superficial fascia of the posterior aspect of the arm and its terminal filaments can generally be traced as far as the olecranon.

Upper external cutaneous. This nerve though described in the textbooks was very seldom found, and it was not considered of sufficient importance to warrant any records being taken of it.

Lower external cutaneous. Arises 13·95 cms. (·457). (Fig. 6.)

A large nerve trunk, of interest as being the only branch of importance arising from the musculo-spiral trunk in the musculo-spiral groove. Its point of origin is so extremely variable (7·11 cms.–28·87 cms.) that the average is of little value. This variability is largely due to the fact that this nerve is the branch of the musculo-spiral most easily "split up" from the main trunk. Probably the nerve fibres are arranged in their own sheath of perineurium in the axilla in all cases. This bundle has frequently been observed to arise in common with the nerve to the outer or inner heads of triceps or even in common with both these branches.

From its origin it proceeds down the musculo-spiral groove in company with the main trunk, and at the lower end of the groove it turns outwards to pierce the deep fascia immediately behind the external inter-muscular septum. Exceptionally it becomes cutaneous by piercing the lower and outer fibres of the triceps. After piercing the deep fascia it runs obliquely distally and medially to gain the middle of the posterior aspect of the forearm. It then runs vertically down the forearm and can be traced as far as the posterior aspect of the wrist-joint. The position of the nerve on the posterior aspect of the forearm varies between the radial border and the axial line. The nearer it runs to the radial border of the forearm the more likely it is to communicate with the posterior division of the musculo-cutaneous (see fig. 4).

9. RADIAL NERVE

This is the smaller of the two terminal divisions of the musculo-spiral and arises, therefore, where this nerve terminates on the anterior aspect of the outer side of the elbow on an average horizontal level with the tip of the external condyle. It runs down the forearm along a line continuous with that of the terminal portion of the musculo-spiral trunk. Just below its origin it is in intimate relation with the front of the elbow-joint and the head of the radius. From its origin it lies under the supinator longus muscle, which relation it maintains to a point ·5 cm. above the junction of middle and lower thirds of the forearm. There, on account of the slight lateral obliquity of its course, it appears behind the posterior border of the supinator longus tendon and

almost immediately afterwards pierces the deep fascia. It then proceeds vertically downwards in the superficial fascia to its cutaneous termination in the hand and fingers. This cutaneous distribution has been considered in the description of the sensory supply of hand and fingers when the ulnar nerve was dealt with.

Some interesting anomalies were found in connection with this nerve:

(*a*) On both sides of one body the radial was completely absent.

(*b*) In another case the supinator longus muscle was inseparably fused with the extensor carpi radialis longior and the tendon of the combined muscles was inserted into the base of the second metacarpal bone. Here it was noticed that the nerve pierced the fused tendons marking off the portion of the tendon corresponding to the supinator longus superficially from that portion corresponding to the extensor carpi radialis longior deep to the nerve.

(*c*) In three cases the motor branch to the extensor carpi radialis brevior arose from the radial trunk.

(*d*) One radial nerve was observed to wind round the mesial margin of supinator longus opposite the elbow-joint and to pass down the forearm superficial to this muscle.

The most important point, for practical purposes, in the course of this nerve is that at which it becomes cutaneous by appearing from under the tendon of the supinator longus. This point was found to average 15·53 cms. down the average forearm of 24·04 cms. length, i.e. 8·5 cms. above the tip of the radial styloid process, which will be seen to be just above the junction of middle and lower thirds of the forearm. This point varied between 12·52 cms. and 18·28 cms.

The communications of the radial nerve at the wrist-joint have been discussed in section 3, when describing the musculo-cutaneous nerve.

10. POSTERIOR INTEROSSEOUS NERVE

This nerve normally contains all the motor fibres remaining in the musculospiral nerve when it divides in front of the external condyle of the humerus. These fibres are distributed by the posterior interosseous nerve to all the muscles on the back of the forearm, except in the anomalous cases mentioned, in which the radial supplies extensor carpi radialis brevior.

The following measurements have been taken to fix the course of this nerve:

In the average forearm of 24·04 cms., posterior interosseous arises 0·0 (average)			
Nerve to extensor carpi radialis brevior arises	1·82 cms.	(·076)
„ „ enters	6·10	„	(·254)
Posterior interosseous enters supinator brevis	4·05	„	(·169)
„ leaves „	7·09	„	(·295)
Dips below extensor longus pollicis	13·69	„	(·570)

Two minor anomalies of this nerve are worthy of mention:

(1) In three cases the motor fibres to the extensor carpi radialis brevior

were carried down in the radial nerve for a short distance before being given off to the muscle.

(2) In three cases the posterior interosseous, in its course down the back of the forearm, crossed the superficial aspect of the extensor longus pollicis instead of dipping down normally at the upper border of this muscle to reach its deep aspect.

Nerve to the extensor carpi radialis brevior. This is the first branch of the posterior interosseous nerve and the only one arising on the front of the forearm. As just mentioned, this nerve may occasionally come from the radial trunk. It arises 1·82 cms. down the forearm and proceeds distally and very obliquely laterally. Just before it reaches the muscle it splits into numerous bundles of fibres which enter the anterior border of the muscle along a vertical line of considerable extent. The horizontal level of this point of entry is 6·10 cms.

Nerves to the supinator brevis. These are numerous short branches which arise while the posterior interosseous trunk is in relation to the anterior, lateral and posterior aspects of the neck and upper part of shaft of the radius. The nerve trunk takes this course amidst the fibres of the supinator brevis, thus dividing this muscle into a superficial and a deep portion.

The posterior interosseous leaves the supinator brevis on the back of the forearm a considerable distance above the lower border of that muscle. Its exit is bounded above by the lower margin of a well-defined tendinous arch which is developed on the posterior surface of the supinator brevis.

The course of this nerve through the supinator brevis muscle is of clinical importance. It is firmly bound down in this region to the neck and upper part of the shaft of the radius by the superficial fibres of supinator brevis and consequently can hardly escape injury in fracture of this portion of the radius. This relationship to bone is maintained from the point where the nerve enters the muscle on the anterior aspect of the forearm to the point where it leaves it on the posterior aspect. The vertical distance between these two points is over 3 cms. and so the posterior interosseous nerve is extremely vulnerable in lesions of the radius anywhere between 4·04 and 7·09 cms. down the forearm.

The posterior interosseous leaves the supinator brevis 7·09 cms. down the forearm as a flat band of nerve fibres of considerable width. Almost immediately after its appearance this band gives off the majority of its fibres as a bundle which runs horizontally backwards to sink into the deep aspect of the superficial extensor muscles.

This large posterior leash of nerve fibres may therefore be considered as arising 7·5 cms. down the forearm. Before it reaches its muscles it breaks up into at least four distinct branches. Two of these sink immediately into extensor communis digitorum. One, slightly longer than its companions, has a short oblique course downwards and medially to end in extensor minimi digiti. The last of the four constant branches has a short but distinct course practically horizontally inwards to end in extensor carpi ulnaris. Very inconstantly a fifth branch may be traced still further inwards to terminate

in the lower fibres of the anconeous muscle. On account of their practically horizontal direction backwards these branches are very short and their level of entry to their muscles practically corresponds with their level of origin as a bundle from the main trunk (7·5 cms.). As an exception to this general rule, the nerve to the extensor minimi digiti, by the obliquity of its direction, enters its muscle at a slightly lower level.

The main trunk of the nerve, reduced to less than half its size, now runs vertically down the forearm between the superficial and deep extensor muscles as far as the upper border of the extensor longus pollicis. It lies in this portion of its course well to the radial side of the axial plane of the forearm and rests from above downwards on the lower fibres of the supinator brevis, extensor ossis metacarpi pollicis and extensor brevis pollicis.

Nerves to the extensor ossis metacarpi pollicis. These are generally two short stout branches which arise from the main trunk as it is lying on the muscle, and consequently they have practically no extra-muscular course.

Nerve to the extensor brevis pollicis. A fine filament arising from the main trunk as it lies on the muscle, which sinks into the muscle immediately.

The main trunk reaches the upper border of extensor longus pollicis 13·69 cms. down the forearm and normally dips below this muscle to gain the interosseous membrane. It has already been mentioned that in three of the dissections it continued its downward course superficial to this muscle.

Nerve to the extensor longus pollicis. This is a bundle of fibres of some size, which arises just before the nerve passes deep to the muscle. The branch breaks up into two or three filaments which enter the upper (or lateral) border of the muscle over an area of considerable vertical extent.

Nerve to the extensor indicis proprius. This muscle is supplied by a slender filament which arises from the posterior interosseous nerve whilst this trunk descends on the interosseous membrane. This branch runs backwards to enter the deep surface of its muscle. The nerve to the extensor indicis proprius is always described as the last muscular branch of the posterior interosseous, but the posterior interosseous may occasionally have still another muscle to supply. In three cases of this series a muscle has been observed which may be called the extensor medii proprius. This muscle when present receives the last motor fibres of the posterior interosseous nerve and, on account of its size and its possible clinical significance, seems worthy of description.

Extensor medii digiti proprius muscle (fig. 7). This muscle has been found in three out of the 26 adult limbs examined in this work.

It arises from the posterior and lateral surfaces of the ulna below the extensor indicis proprius and from the inter-muscular septum separating it from the extensor carpi ulnaris. In one case its fleshy belly of origin was partially fused with that of extensor indicis, but in the other two it was quite distinct. The fleshy belly gives place to a tendon which runs under the posterior annular ligament in company with the extensor communis and extensor indicis tendons. The tendon then passes obliquely over the dorsum of the hand medial to that of extensor indicis and deep to the extensor communis tendons,

and gains its insertion by joining the ulnar side of the dorsal expansion of the long extensor tendon to the middle finger.

This muscle, judging from the description of its insertion, is the musculus Manieux described by Le Double (8), but this author described its origin as from the back of the carpus and in no description have I read of its possible origin from the ulna.

It is of morphological interest, since it may be considered either (1) as the reappearance of an atavistic short extensor of the middle finger, or

Fig. 7. Extensor medii digiti proprius muscle.

(2) as an example of what Wood-Jones (6) describes under the term of "progressive variabilities." A quadruped, such as the cat, has a special short extensor to each of the digits of its forelimb and these are used as muscles of progression. In bipedal man the forelimb is not used for progression and therefore these short extensors lose their function. Those to the middle and ring fingers disappear and the remaining three are retained and modified to subserve other uses. The medius is probably the next in importance to the thumb, index and little fingers and would therefore be the next most likely to require an individual short extensor. It is just possible then, that the reappearance of this special short extensor of the medius may be a progressive

stage in the development of the human hand. The well-defined appearance of this muscle three times in 26 cases seemed to me a somewhat excessive percentage for a pure atavism.

The posterior interosseous nerve terminates on the dorsum of the carpus in a swollen extremity from which appear small filaments for the supply of the carpal joints.

Tables of Measurements

It is hoped that these Tables may prove of clinical value. They are compiled from over 700 measurements of 25 adult limbs. Extreme anomalies, which would invalidate the ratios, have been excluded.

The principle of these measurements has been explained in the introduction and little more remains to be said.

Two vertical measurements have been taken. One, from the tip of the acromion process to the tip of the external condyle of the humerus, for nerves of the upper arm, may conveniently be spoken of as the "A measurement"; the second, from the tip of the external condyle to the tip of the styloid process of the radius, which may be called the "B measurement," and is for nerves in the forearm.

In the 25 limbs under consideration

The average length of A measurement = 30·5 cms.

„ „ B „ = 24·04 „

Column 3 gives the average ratio of the total A or B measurement where the important point on the nerve is situated. Column 1, which gives the horizontal level of this point down the average arm or forearm, is obtained, therefore, by multiplying column 3 by 30·5 or 24·04 as the case may be.

Columns 4 and 5 give the maximum proximal and distal variabilities found of the average ratio, column 3.

The clinical value of these tables can best be shown by an example.

The clinician may wish to know as accurately as possible where the nerve to the supinator longus arises. He measures the upper arm of his patient and gets an "A measurement" of 32·0 cms. He multiplies this by the average ratio, ·827 in this case,

$$\cdot 827 \times 32 = 26 \cdot 46 \text{ cms.}$$

Therefore, he will expect to find the nerve to the supinator longus arising in this patient at a horizontal level 26·46 cms. vertically below the tip of the acromion process.

He has however to take into account the variabilities of this origin. Applying his A measurement to the maximum proximal and distal variabilities he gets

$$\cdot 742 \times 32 = 23 \cdot 74 \text{ cms.}$$

$$\cdot 900 \times 32 = 28 \cdot 80 \text{ cms.}$$

The variability in this case is, therefore, 5·06 cms. or approximately 2 inches.

Before leaving this section I wish to acknowledge the great assistance I have obtained from Mr Burnet, a student of Engineering at the University of Manchester. His work of averaging and checking the mass of figures, which the compilation of these tables entailed, has been very helpful.

11. TABLES OF AVERAGE MEASUREMENTS AND THEIR VARIABILITIES

	Average distance in cms.	Arm (A) or fore-arm (B)	Average ratio	Variability of ratio	
				From	To
I. *Musculo-cutaneous Nerve:*					
Nerve to coraco brachialis ... ... arises	4·76	A	·156	0·0	·283
" " " ... ... enters	7·35	A	·241	·096	·410
Nerve to biceps ... ... arises	12·99	A	·426	·357	·533
" " ... ... enters	15·28	A	·501	·426	·616
Nerve to brachialis anticus ... ... arises	17·32	A	·568	·400	·650
" " " ... ... enters	20·27	A	·665	·616	·746
Cutaneous division ... ... arises	17·32	A	·568	·400	·650
II. *Median Nerve:*					
Nerve to pronator radii teres ... ... arises	1·0–2·0	B	Variability too great to give reliable ratios. See text		
" " " ... ... enters	1·5–2·0	B			
Nerve bundle to common flexor mass:					
Upper limit of origin	2·08	B	·086	0·0 (B)	·213
" " entry	2·76	B	·115	·037	·340
Lower limit of entry	5·05	B	·210	·143	·425
Branch to index belly flexor sublimis digitorum arises	12·0 +	B	See text		
Anterior interosseous ... ... arises	5·24	B	·218	·130	·314
III. *Circumflex Nerve:*					
Supplies deltoid	6·98	A	·229	·161	·290
IV. *Ulnar Nerve:*					
Branches to flexor carpi ulnaris:					
(i) Nerve to olecranon head ... ... arises	·90	B	·037	0·0 (B)	·115
" " ... ... enters	2·08	B	·087	·020	·200
(ii) Primary nerve to condylar head ... arises	1·62	B	·067	·020	·120
" " " ... enters	2·99	B	·125	·060	·204
(iii) Secondary nerve to condylar head ... arises	2·25	B	·093	·087	·100
" " " ... enters	4·88	B	·203	·193	·213
Nerve to flexor profundus digitorum ... ... arises	3·07	B	·127	·040	·225
" " " ... ... enters	5·54	B	·230	·128	·311
Dorsal cutaneous nerve ... ... arises	17·06	B	·709	·420	·854
" " ... Appears behind flexor carpi ulnaris	20·95	B	·871	·700	·960
V. *Musculo-spiral Nerve:*					
Branches to triceps:					
(i) Nerve to long head ... ... arises	7·11	A	·233	·161	·333
" " ... ... enters	11·30	A	·370	·308	·441
(ii) Ulnar collateral ... ... arises	9·53	A	·312	·179	·419
" " ... ... enters	18·17	A	·595	·431	·800
(iii) Nerve to outer head ... ... arises	10·13	A	·332	·293	·393
" " ... ... enters	14·62	A	·479	·342	·643
(iv) Nerve to inner head ... ... arises	11·21	A	·368	·300	·467
" " ... ... enters	18·26	A	·599	·517	·800
Lower external cutaneous nerve ... ... arises	13·95	A	·457	·233	·750
				See text	
Nerve to supinator longus ... ... arises	25·23	A	·827	·742	·900
" " ... ... enters	28·26	A	·927	·855	0·0 (B)
Nerve to extensor carpi radialis longior ... arises	26·79	A	·878	·786	·935
" " " ... enters	Average immediately proximal to tip of external condyle. See text				
Musculo-spiral nerve ... ... ends	Average level is tip of external condyle. See text				
VI. *Radial Nerve:*					
Appears from under tendon of supinator longus	15·53	B	·646	·521	·761
VII. *Posterior Interosseous Nerve:*					
Nerve to extensor carpi radialis brevior ... arises	1·82	B	·076	0·0	·130
" " " ... enters	6·10	B	·254	·160	·339
Posterior interosseous trunk enters supinator brevis	4·05	B	·169	·120	·245
Posterior interosseous trunk leaves supinator brevis	7·09	B	·295	·240	·358
Trunk dips below extensor longus pollicis ...	13·69	B	·570	·456	·667

12. SUMMARY AND CONCLUSION

An attempt has been made in the text of this paper to emphasise points of clinical importance in the distribution of the nerves of the upper limb. In many cases it has been possible to support the anatomical findings by analyses of clinical groups of cases kindly given me by Prof. J. S. B. Stopford. Most of these analyses have been referred to in the text, so that it is only necessary to give a very brief tabulated summary of the main conclusions arrived at from these observations.

I. Variability of Distribution of Nerve Branches

As the nerve branches show such marked individual variability in their distribution no rules can be laid down. Each branch of each nerve must be taken separately and its variability worked out from the Tables before any accurate conclusion can be arrived at as to its variability. It is interesting to note that the minimum variability of any branch is 4·5 to 5·0 cms., which represents approximately a variation between an inch above and an inch below the point obtained for the average ratio. Variations so extreme as to fall under the heading of anomalies have been excluded from the Tables.

A clinical matter of importance, in which these measurements should be of assistance, deals with the question of prognosis in nerve injuries. It is often difficult to judge by clinical examination before operation as to the length of nerve involved in and devitalised by callus or scar tissue, etc. Upon the length of nerve which will require to be resected at operation depends the important question as to whether or not end-to-end suture will be possible. Reference to the Tables will, in many cases, give the surgeon a definite idea in centimetres of the length of nerve likely to require removal.

II. Subdivision of the Brachial Plexus

The brachial plexus may be subdivided by a vertical line drawn 7·75 cms. from the lateral borders of the lower cervical vertebral bodies or by a similar vertical line 6·75 cms. lateral to the common carotid artery at the root of the neck. Such a line, where it cuts the plexus, divides the trunks from the cords with certain modifications of the usual nomenclature as described in the text. This line has the great advantage of excluding the clavicle as a basis of subdivision.

III. Anterior Thoracic Nerves

Both these nerves have a very high origin from the brachial plexus and should be considered anatomically and clinically, as branches of the nerve trunks and not of the nerve cords.

IV. Communication between the outer and inner cords

In at least 57 per cent. of cases the ulnar nerve obtains fibres from the seventh cervical root by means of a communication which it receives from the inner aspect of the outer head of the median.

V. Anomalies of Musculo-cutaneous Nerve

In a small proportion of cases the branches of this nerve arise direct from an undivided outer cord.

VI. Muscular Distribution of the Musculo-cutaneous

This is completed in the upper two-thirds of the brachium. A lesion of the main trunk distal to 2·0 cms. below the middle of the upper arm will cause no paralysis. Clinical evidence shows that a sensory lesion of the musculo-cutaneous is five times as common as a mixed lesion.

VII. Communication between Musculo-cutaneous and Radial Nerves at the Wrist-Joint

This was absent in two out of seven cases and was seen to vary extremely in size when found. The interchanged fibres are presumably distributed in the branches of the radial nerve.

VIII. Anomalies of Origin of Median Nerve

The position at which the outer head joins the inner head of this nerve shows marked variability but, generally, at least a number of the fibres of the outer head join the inner head at the normal level.

IX. Nerve to pronator radii teres

This nerve seldom arises proximal to the elbow-joint.

X. Nerve to index belly of flexor sublimis digitorum

A branch, frequently present, which arises in the lower half of the forearm and sinks into the deep aspect of this belly. Occasionally it supplies the medius belly of the muscle.

XI. Muscular Distribution of Median Nerve in the hand

Besides supplying the abductor and the opponens pollicis muscles this nerve also supplies the superficial slip of that portion of flexor brevis pollicis which is inserted into the radial sesamoid bone and the radial side of the base of the first phalanx of the thumb.

XII. Circumflex Nerve

The most constant nerve of the upper limb in origin, course and distribution. Its anterior terminal division is purely motor to the deltoid. The posterior division takes up a lower horizontal level than that maintained by the anterior division.

XIII. Nerves to flexor carpi ulnaris

These vary from two to four in number. They all enter the muscle high up in the forearm, the point of entry of the lowest being 4·88 cms. Only occasionally does the highest of these branches arise in the upper arm, but this infrequent

high origin will account for those exceptional cases in which the flexor carpi ulnaris is only paretic after an injury to the ulnar nerve trunk, where it lies between the olecranon process and the internal condyle.

XIV. Nerve to flexor profundus digitorum

A single stout trunk, with an extra-muscular course of about an inch, and not the two distinct bundles of fibres, one for each ulnar belly of the muscle, as described by Poirier(7).

XV. Dorsal Cutaneous Branch of Ulnar Nerve

Origin very variable. Point where it becomes cutaneous at the medial border of the flexor carpi ulnaris reasonably constant and just over an inch proximal to the tip of the styloid process of the radius, i.e. approximately half an inch above the styloid process of the ulna.

XVI. Digital Cutaneous Distribution of Ulnar Nerve

On the palmar aspect the ulnar nerve gives the classical supply of $1\frac{1}{2}$ fingers in 80 per cent. of cases.

The dorsal cutaneous branch of the ulnar supplies $2\frac{1}{2}$ fingers in 75 per cent. of cases.

XVII. Communication between Ulnar and Internal Cutaneous Nerves

These nerves have been seen to communicate in the upper arm but not in the region of the wrist-joint.

XVIII. Termination of Musculo-spiral

Variability from approximately 4 cms. above to 4 cms. below the tip of the external condyle. This bony point gives a good average level of termination.

XIX. Nerve-supply of triceps

This muscle has four distinct bundles of fibres from the musculo-spiral nerve. For practical purposes they all arise in the upper third of the arm before the main trunk enters the musculo-spiral groove. The two nerves for the inner head have the longest extra-muscular course.

XX. Discretion of bundles of Nerve fibres in the Musculo-spiral

The individual bundles of fibres of this nerve are arranged and receive their own sheaths of perineurium in the lower part of the axilla. Consequently the branches of the musculo-spiral are very easily split up from the main trunk, and suture of individual bundles ought to be easily practicable.

XXI. Ulnar Collateral Nerve

This is the smaller and less important branch to the inner head of the triceps.

XXII. Branch of Musculo-spiral to Brachialis Anticus

Probably an afferent nerve-path.

XXIII. Cutaneous Branches of Musculo-spiral

Internal cutaneous branch generally arises from one of the nerves to the long head of triceps.

Upper external cutaneous branch was very seldom found.

Lower external cutaneous branch supplies the skin of the back of the forearm as far as the wrist. It occasionally communicates with the musculo-cutaneous. It is the branch of the musculo-spiral most easily split up from the main trunk.

XXIV. Radial Nerve

This becomes cutaneous as a rule just above the junction of middle and lower thirds of the forearm, approximately 3½ inches proximal to the tip of the radial styloid process.

XXV. Nerve to the Extensor Carpi Radialis Brevior

Occasionally this motor nerve arises from the radial trunk.

XXVI. Relation of the Posterior Interosseous Nerve to Radius

The posterior interosseous nerve is an intimate relation of this bone throughout its course through the supinator brevis muscle. As its relation to the muscle has a vertical extent of over 3 cms. it can hardly escape injury in fracture of this portion of the radius.

XXVII. Extensor Medii Digiti Proprius Muscle

A well-defined muscle-belly present in three out of 26 cases.

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ON THE DEVELOPMENT OF THE FISSURAL AND ASSOCIATED REGIONS IN THE EYE OF THE CHICK, WITH SOME OBSERVATIONS ON THE MAMMAL

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It is a well-known fact that in embryonic eyes, both avian and mammalian, the point of attachment of the optic stalk and of the early optic nerve is to the extreme lower part of the optic cup, while in the grown eye it is practically half-way up the posterior surface of the globe. What then is the mechanism whereby the lower portion of the retina is formed? There is evidence to show that growth takes place below the level of the optic stalk, and that in the formation of the lower portion of the retina the choroidal fissure and parafissural regions are concerned. The closure of the choroidal fissure takes place very early in the mammalian eye, but in the large eye of the chick embryo the process is relatively slower and can be more easily observed.

In the eye of the chick embryo the choroidal fissure is at first very short and directed vertically downwards. Its margins apparently come together first in the intermediate portion, leaving the proximal part open for the ingrowing vascular mesoderm. This mesoderm, which in differentiation very soon shows one or two definite thin-walled blood vessels, at first occupies the whole of the interval between the intermediate closed portion and the upper end of the fissure, and, after traversing the lower part of the globe, passes out again at the distal opening in the fissure at the pupillary margin.

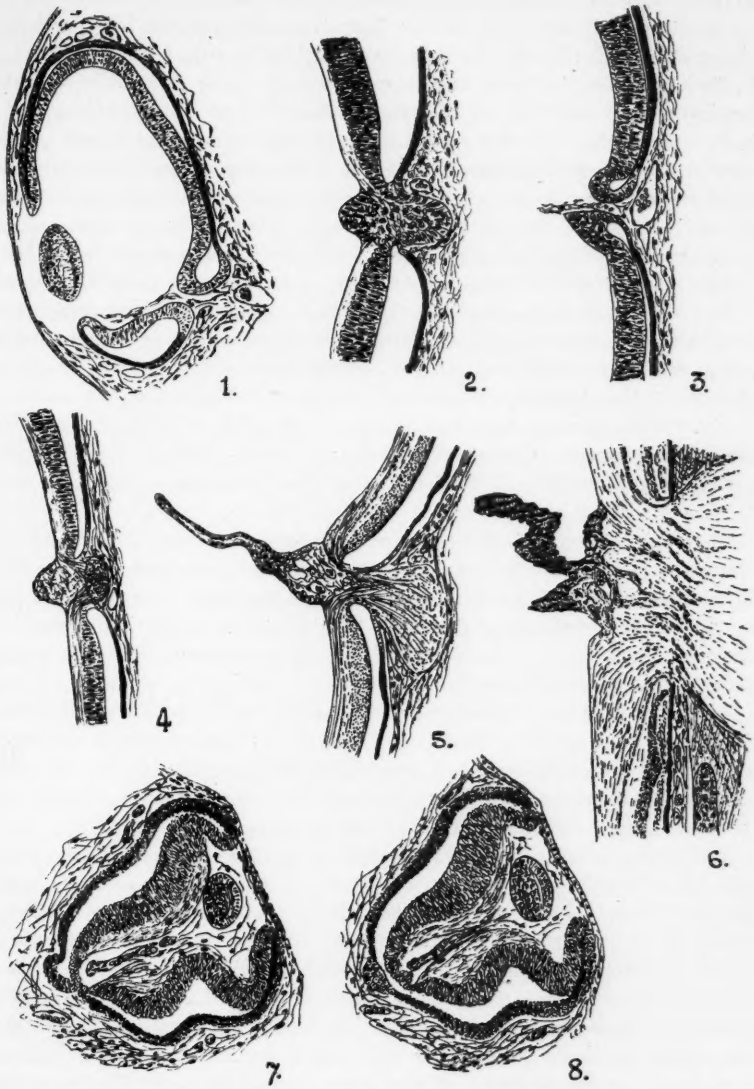
The growth of the lower part of the retina apparently takes place by extension of the margins of the cleft and neighbouring areas in the form of two processes or cornua which extend downwards, curving of course outwards with the retinal concavity to reach the pupillary margin. Further, it appears probable that the growth of these two cornua is not exactly equal, the posterior or malar one increasing slightly more rapidly than the anterior, with the result that the line of the fissure becomes altered as growth proceeds. The direction is at first vertically downwards, but in the adult bird the line of the fissure, which is represented by the line of nerve fibres entering the so-called *cauda* of the nerve, runs downwards and forwards. In a series of chick embryos of increasing age this alteration in direction can be seen to take place gradually, the angle decreasing in successive specimens from a right angle in the earliest embryos examined to about 70° with the horizontal in the adult bird. It is

also noteworthy that the nerve fibre layer of the developing retina appears first in the region above the optic stalk, namely in the oldest part of the retina, and thence extends gradually downwards on either side of the fissure, the area possessing nerve fibres being at one stage slightly more extensive on the malar side of the cleft than on the nasal.

The adult bird, however, differs from the mammal in that in the former the blood vessels enter the eye some distance below the nerve attachment, and also in that some of the nerve fibres pass out of the globe below the nerve attachment and run up to this on the back of the eye: these constitute the *cauda*. The fissure in the bird, however, as will be apparent later, originally exists proximal to the point of entry of the vessels, and, as in the mammal, the upper end of the fissure is included in the nerve attachment.

At an early age in the chick, possibly as a result of quicker growth of the inner, non-pigmented, layer of the optic cup, this layer becomes everted, so to speak, in the lips of the fissure. This condition is shown in fig. 1, which represents a section through the eye of a chick embryo of about four days. The fissure is still open in its entire length and, though very little pigment is as yet present in the outer layer of the cup, the everted portion of the inner layer at the margins of the cleft can be recognised by its similarity in thickness and type of cell to the true inner layer. This eversion occurs in the upper part of the cleft first, and is always more marked here. The everted area elongates with the elongation of the fissure, but not co-extensively with it and so never reaches the pupillary margin. At first the entering vessels occupy the whole of the region of the fissure bordered by this everted area, but later, as the margins of the fissure come together, the entering vessels lie towards the lower end of the area. From their point of entrance they pass forwards in the vitreous, forming a vascular septum stretching across the lower part of the globe to their original point of exit from the cleft just below the pupillary margin. This distal portion of the fissure soon closes and the vessels are cut off here and gradually become shorter. Their subsequent fate will be discussed later.

The upper part of the cleft must now be considered. It is easily seen that when this upper part closes fusion takes place, owing to the eversion just described, between two portions of the non-pigmented inner layer only. After obliteration of the cleft there remains an area of non-pigmented (originally inner) layer on the outer surface of the globe, this area being directly continuous at its edges with the true outer pigmented layer some little distance away from the fissural line. This condition is shown in fig. 2, which is a transverse section (from a slightly older chick) through a portion of the back of the globe including the margins of the cleft in the region between the point of attachment of the optic stalk above and the entering vessels below. It will be seen that fusion takes place between comparatively large areas of inner layer, so that two projections or ridges are formed by the heaping up of this layer, one, anterior, projecting into the globe, the other, more marked, on the posterior surface, continuous at its base with the pigment layer. Fig. 3 shows the mode



Figs. 1–5. Sections through embryonic chick eyes. Fig. 6. Adult hen. Figs. 7 and 8. 15 mm. human embryo. (From camera lucida drawings.)

of fusion of the lips of the cleft in the region of the entering vessels. It will be seen that the overgrowth of the inner layer is not sufficiently marked here to give rise to definite eversion and the formation of a posterior ridge, but that it is great enough to form the anterior projection and that here, as in fig. 2, the fusion occurs between two non-pigmented areas only. The anterior prominence fades away below the vessels. Thus it comes about that in a fresh chick embryo the line of the fissure stands out as a white streak on the superficial surface of the large pigmented eye. Developing nerve fibres adjacent to the sides of the fissure will grow into this posterior non-pigmented area since it is in origin directly continuous with the fibre-bearing inner retinal layer. This morphological continuity is well seen in early chicks where there is some attempt at the formation of a rod and cone layer to be seen in the everted portion. This is indicated in fig. 2. This appearance is of short duration since the cells are soon obliterated by the ingrowing nerve fibres, which become visible as bundles running up on the back of the globe to the nerve attachment, thus later forming the *cauda* of the adult nerve.

Fig. 4 shows a later stage through the same region as in fig. 2. The nerve fibres can be seen passing into the projection on the posterior surface, which now consists of bundles of fibres forming the *cauda* and running up to the nerve attachment.

These phenomena of closure as seen in the upper part of the cleft are intimately connected with the development of the *pecten* and some mention must be made of this in explaining the subsequent fate of the margins of the fissure. It has already been shown that the posterior projection of the non-pigmented layer in the upper part of the fissure provides the path for the fibres of the *cauda* of the nerve.

The fate of the anterior ridge remains to be dealt with. The lower portion of this, below the entering vessels, very soon after fusion of its two component lips and before the appearance of nerve fibres in this region, becomes flattened and takes on the character of the retina on either side of it and no trace of the situation of the ridge can be subsequently demonstrated.

The upper portion (fig. 2), which will be referred to as the *crista intraocularis*, behaves differently. When the developing nerve fibres grow towards the region of the cleft (figs. 2 and 4) they do not reach the posterior everted projection by remaining on the surface and entering along the line of fusion, but they begin to sink into the substance of the inner (retinal) layer along the base of the *crista* and so by taking a more direct route they cut off, as it were, the portion of the inner layer which forms the ridge, and separate it from the deeper strata. The cells of the *crista intraocularis* never show any attempt at differentiation into nervous retinal elements. At first (before the appearance of the nerve fibre layer) the tissue appears to be spongioblastic in nature. Later, as the ridge becomes cut off by the ingrowing nerve fibres, it takes on a more reticular appearance, the cells becoming smaller and somewhat stellate and the whole structure appearing as a loose meshwork of cells and fibrils covered and

limited on its free or vitreous surface by the *membrana limitans interna* and in relation on the inner side of this again with the hyaloid membrane, which is always firmly adherent to the ridge.

By this time a change has taken place in the arrangement of the blood vessels entering the eye. The vascular septum which at first passed through the lower part of the globe entirely disappears. The proximal portion of the vessel however remains and now enters the eye at the lower end of the *crista intraocularis*. This ridge of loose reticular tissue, described above, now becomes vascularised by branches of the vessel running in its substance towards the upper end. These branches increase in number and the *crista* becomes more marked and develops a sharp apex. The ridge now shows in its lower part as the primitive unplicated pecten. Growth proceeds from below up and the pecten develops as a septum growing out into the vitreous (the hyaloid membrane being always firmly attached to its sides and apex) and consisting of ramifications of the proximal part of the original choroidal vessels enclosed in a loose stroma, neuroglial in nature, derived from the portion of the fused lips of the fissure cut off by the growing nerve fibres. This condition can be seen in fig. 5, which should be compared with the preceding figure, where the precursor of the pecten can be clearly seen in the form of the *crista intraocularis*. Later the pecten grows rapidly, becomes many times folded upon itself in a complicated manner, and pigment is developed in it. Fig. 6 shows a section through the extreme upper end of the pecten in an adult hen's eye. It can be easily seen that it occupies the position of the *crista intraocularis* in the embryonic eye and that its "roots," if the term may be used, are directly continuous with the supporting neuroglial septa of the optic nerve, in which, however, there is no pigment. It is in this way easy to understand that the pecten *ex origine* is attached along a line extending between the optic nerve and the entering vessels.

Examination of various embryos shows that the earlier stages in development of the chick's eye have their parallel among the mammalia. The eversion of the inner layer in the upper part of the cleft occurs in mammals but to a much less extent than in the bird. The position of the *arteria centralis retinae* shows that this eversion must be of the lips of the fissure. Figs. 7 and 8 show the condition in the 15 mm. human embryo. Fig. 7 shows the cleft with the entering vascular tissue. It will be seen that the out-turning of the inner layer is marked. Fig. 8 shows the condition immediately below that shown in fig. 7 in the same embryo. The two everted inner layers have come together and fused, forming a small mass of non-pigmented cells continuous with the outer pigmented layer (the parallel of the larger structure in the chick). These non-pigmented cells do not appear connected with the inner layers here since in man no nerve fibres grow into this everted region and no *cauda* is formed to the optic nerve.

The condition can be seen best in human embryos of 13 mm. and 15 mm. It is extremely small in the 16 mm. embryo and in the 18 mm. it has practically

disappeared. It is very well marked in early mouse embryos. There is no trace of the formation of a true *crista intraocularis* in the mammalian eye. It is true that when the inner layers of the retina fuse below the *arteria centralis retinae* in the mammal the site of fusion remains for a very short period as a slight projection into the vitreous which, like the similar area below the vessels in the chick, soon becomes flattened and indistinguishable from the retina on either side of it. There is, however, no sign of a *crista* above the vessels, and the nerve fibres pass into the nerve head on the inner surface of the inner layer and do not sink deep to it in any place.

The possible causes of this difference of behaviour of the avian and mammalian cleft margins are of course somewhat obscure, but may be associated with relative differences in dimensional growths of the lower portions of the retinal fields and also with the relation in time between the appearance of nerve fibres in various areas and the closure of the cleft. It is hardly necessary to say that the eversion of the inner layer must occur while the cleft is, potentially at least, still open.

In conclusion, I wish to express my thanks to Professor Frazer both for the loan of much valuable material and for his encouragement and advice in the preparation of this paper.

THE EVOLUTION OF THE VERTEBRATE ENDOSKELETON

AN ESSAY ON THE SIGNIFICANCE AND MEANING OF SEGMENTATION IN COELOMATE ANIMALS

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THE EVOLUTION OF THE VERTEBRATE ENDOSKELETON

When investigating the morphology of the vertebrate head, I found it necessary to discover the morphological principles on which the segmentation of the body is founded. This essay is one of the results of this investigation, and its object is to show what has determined the segmented form in vertebrate animals. It will be seen that the segmented form in vertebrates results from a condition which at no time occurs in vertebrate animals. This condition is a form of skeleton found only in animals lower in the scale of organisation than vertebrates, and has the characters of a space containing water. This space is the Coelomic Cavity. The coelomic cavity is the key to the formation of the segmented structure of the body, and is the structure that determines the vertebrate form.

The coelomic cavity is present in a well defined state from the Annelida upwards, so that in annelides it is performing the functions for which a coelom was evolved. It is, however, necessary to observe the conditions prevailing among still lower forms to see why a separate cavity was formed in animals, which became the means of raising them in the scale of organisation, and ultimately leading to the evolution of the vertebrate animal.

I therefore propose to trace the steps in evolution by which, I presume, the coelomic cavity originated, and then show how it or its modifications have been the basis on which the whole vertebrate structure of animals is founded. In demonstrating this the various steps or stages in the evolution of the vertebrate endoskeleton will be indicated clearly.

In the evolution of the vertebrate endoskeleton five distinct stages occur. These are:

1. The Hydroskeleton.
2. The Hydrostatic skeleton.
3. The Sclerotome skeleton.
4. The Neural skeleton. (Notochord.)
5. The Neuro-muscular skeleton. (Vertebrate skeleton.)

1. THE HYDROSKELETON

In the large and lowest group of the Metazoa, namely the Coelenterata, we, for the first time find animals possessing three distinct kinds of tissues. The outer of these is the ectoderm, and is more or less epithelial. This is a protective and receptive layer of cells which are modified in many ways to perform both of these functions. In all animals those structures which keep the animal informed about its surroundings, and which control its reactions to them, are derived from this layer. The middle layer or mesoglea is a somewhat structureless tissue developed to very different degrees of organisation in different Coelenterates. It represents the mesoderm of higher animals in which it comes to form the bulkiest portion of the animal tissues. The inner layer is the endoderm. It is the layer that nourishes the animal, and it lines a cavity called the enteron. The cells of this layer are principally digestive, but some are arranged for entrapping and killing the animalculae upon which these animals feed, and which are drawn into the enteric cavity with the circulating water. The enteric cavity is the digestive and respiratory organ of the animal and it only possesses one opening which serves both for mouth and anus. Around this opening there are muscle fibres arranged to act as a sphincter. This cavity is always kept filled with water, which however, is being constantly changed by the activities of the animal for metabolic purposes. In addition to the physiological characters of this cavity and its contained fluid, we recognise a fact of great morphological importance. This is that the water contained in the enteric cavity has the essential characters of a skeleton. Thus it gives form to the animal, and maintains this form. Being an incompressible fluid it gives the animal's muscle fibres a resisting body to act upon, and so allows of alterations of shape, and in free swimming forms allows of propulsion through the water. When the water, which is the skeleton of the animal, is removed from its enteric cavity, the supporting structure is gone and the animal loses its shape just as when it is dead. This is the hydroskeleton and is the first stage in the evolution of the vertebrate endoskeleton. Fig. 1 shows the conditions present in a hydra polyp where we find the three layers of tissues mentioned above, and the enteric cavity. Where the oral tentacles are hollow the enteric cavity extends into them so that they likewise derive their support from the water in the enteric cavity, and their movements depend upon its presence. Fig. 2 shows the disposition of parts in a medusa form where the umbrella or under surface of the animal contracts upon the water in contact with it as a means of propulsion.

Fig. 3 shows the arrangement of parts in a sea-anemone. The same three layers are present and the enteric cavity; also hollow or solid tentacles. The mouth opening is present and leads down into the enteric cavity through a tubular invagination called the oesophagus. The enteric cavity is incompletely subdivided by a number of longitudinal septa passing from the body wall towards the centre ending in a free margin. Certain of these septa, however,

attach themselves to the oesophagus forming incomplete compartments in the enteric cavity. These cavities extend into the hollow tentacles. On these septa are placed the reproductive glands which discharge their cells into the enteric cavity. These animals also depend upon the water contained in the enteric cavity for the maintenance of their form and for providing a means for their muscles to produce movements, so that here again we find the hydroskeleton in the enteric cavity. This type of skeleton is evidently efficient in its principle, namely, that water is dense and incompressible, but the structure of the animal limits the efficiency of the hydroskeleton by allowing the water to escape easily, which is necessary, as frequent change of water is required by the animal for metabolic purposes.

The enteric cavity here contains the skeleton, digestive, respiratory, excretory and reproductive systems. These are all represented in a very simple

Fig. 1 Fig. 2 Fig. 3

Fig. 1. Diagram of hydra polyp showing enteric cavity which contains the hydroskeleton.
Fig. 2. Diagram of the same parts in a medusa.
Fig. 3. Section through the oesophagus of a sea-anemone showing enteric spaces and mesenteries. After Shipley and MacBride.

form, while in higher animals these systems all become differentiated and specialised.

In concluding the remarks on the hydroskeleton of coelenterate animals, I would again point out that the skeleton is the water contained in the body of the animal. It is this water that maintains the form of the animal, and it is upon this water that the muscles of the animal act in order to effect movements of parts of the body on one another, or the propulsion of the animal as a whole. The skeleton being the water within the body of the animal, and the body cavity never being shut off from the water in which the animal lives, it is not very efficient as a skeleton, and dooms the whole class of coelenterate animals to an aquatic existence. So soon as the animal is removed from the water its skeleton is lost, and it has then no means of maintaining its form, and still less has it any means of continuing its existence.

2. THE HYDROSTATIC SKELETON

In the next stage in the evolution of the vertebrate endoskeleton, the chief disadvantages of the hydroskeleton are overcome by confining the water which forms the skeleton in an enclosed space. This is effected by the complete separation of the enteric pouches from the enteric cavity. The arrangement of the mesenteric septa in relation to the oesophagus or stomodaeum in actinian forms strongly suggests how this could be accomplished as in fig. 3. The continuance of the process by which enteric pouches are formed would result in the complete separation of these pouches from the enteric cavity. This would form a new set of enclosed spaces situated between and separating the enteric cavity from the body wall. I do not propose to do more than suggest such a method of producing these perienteric spaces, for we find a different method obtaining in some other animals. In coelomate animals we are presented with this condition as an accomplished fact. It is this condition that makes animals coelomate, and separates these entirely from the whole group of Coelenterates. It is therefore a condition of the highest importance in the evolutionary history of animals.

These perienteric cavities are present in some form in all animals higher in the scale of organisation than Coelenterates, and the reproductive cells are always produced in their walls, just as they are in the sea-anemone. There may be pores in the body wall of the actinozoon, and also in hollow tentacles, by means of which the reproductive cells can escape to the exterior of the body. In the higher forms more efficient means are adopted for the same purpose.

We have now to deal with coelomate animals which are characterised by having a perienteric space separating the body wall from the enteric cavity which now forms the gut wall. The lowest annelid shares this common character with the highest vertebrate. This perienteric space is the coelomic cavity, and this cavity is of the first importance as a skeletal structure, or, more accurately, as a space containing the skeleton, and it with its derivatives will be described from this point of view. This skeleton of water being enclosed in the coelomic space may be called a hydrostatic skeleton.

The lowest animals possessing this coelomic space are the Annelida, and the most primitive of these present this coelomic space well formed and containing the watery skeleton, which gives these animals definite shape, and upon which its body muscles can act and produce movements and locomotion. In addition, this space is used for purposes of excretion, for which its boundaries are suitably modified, and, as before stated, reproductive cells are shed into it and are subsequently allowed to pass from it to the exterior of the body.

In adult archiannelids, this coelomic space is broken up into two series of compartments. There are two different arrangements for dividing these spaces into compartments. One set consists of two compartments which are antero-posterior or cephalo-caudal in direction, and present a coelomic cavity on either side of the gut from end to end of the animal. The walls of these spaces

form the dorsal and ventral mesenteries of the alimentary tube throughout its entire length in the middle line, while they are related to the body wall peripherally.

This form of coelomic spacing is not found on account of the fact that long flexible tubes of water cannot withstand lateral strain. Some animals, however, do present such a coelom, but it is reduced in comparison with the thickness of the body wall, and it does not contain water.

To prevent lateral strain from distorting the animal, these two coelomic spaces become divided transversely at short intervals by septa, so that there

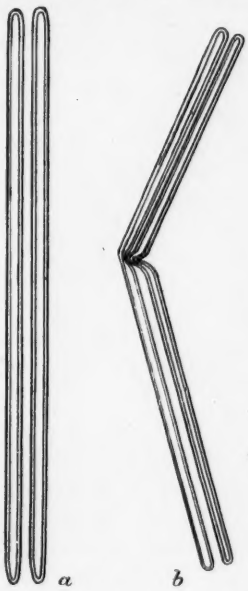

Fig. 4

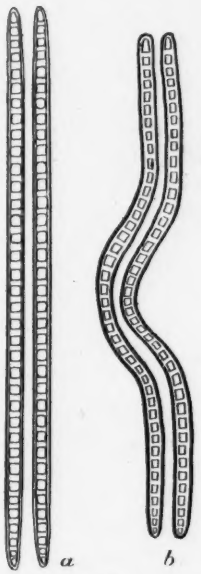

Fig. 5

Fig. 4. (*a*) Supposed primitive coelomic spaces without transverse septa; (*b*) result of such an arrangement in a lateral flexion.

Fig. 5. (*a*) Segmentation of the coelomic space by septa; (*b*) result of lateral flexion under segmented conditions.

are now many compartments whose antero-posterior length is not much greater, if any, than their diameter. These sacs containing fluid are completely shut off from each other, and are arranged in two rows, one on each side of the gut. Figs. 4 and 5 show this. Each enclosed compartment or sac is the exact likeness of those adjacent. They are all serially homologous, for they all have the same fundamental structures; and are all derived in the same way from the same structures. These spaces are always kept filled with water, which forms a permanent endoskeleton, and it acts as such as long as the animal lives. When the animal dies, the water disappears and the form is lost.

The transverse division of the large coelomic cavity into compartments is in obedience to mechanical principles that relate to tubes and their stresses. For a certain thickness of tube wall, support requires to be repeated at certain intervals according to the pressure the tube has to withstand, so that we find coelomic sacs of different diameter and of different antero-posterior length in different animals.

This is the first appearance of what is called Segmentation of the Body in animals. The beginning of this segmentation is this division of the hydrostatic skeleton into segments. This secondarily involves the other tissues in relation to the coelomic spaces, namely, excretory organs, muscular and neural structures, etc.

The segmentation of the hydrostatic skeleton is of the greatest importance to animals possessing such an organ, for we can see that with a skeleton in the form of a long unsegmented tube filled with water the animal would be liable to kink its body after the manner of a flexible tube, and thus produce strangulation of the part of its body behind the distortion. This is prevented by breaking up the skeleton into parts or segments, of which the antero-posterior length is usually less than the diameter.

The segmentation of the hydrostatic skeleton by its influence on other tissues leads to a distinct morphological arrangement, which is a repetition of similar parts. This segmented arrangement allows of a degree of evolution that unsegmented animals do not attain. Thus among coelomates of the chordate class we find mammals have evolved in the highest degree; and among coelomates of the non-chordate class we find the highest degree of evolution presented by the highest group of arthropods.

This segmental arrangement of tissues so necessary in animals with a hydrostatic skeleton is not lost even when the hydrostatic skeleton has been replaced by a more rigid skeleton. Indeed it is retained by the tissues in all the vertebrates, although in no vertebrate animal does a hydrostatic skeleton ever exist. For this reason we find segmentation of the body presented by animals as lowly organised as the simplest annelids, and as highly organised as man.

As secondary morphological changes resulting from the segmentation of the hydrostatic skeleton, we find that each segment of the hydrostatic skeleton is separately related to that part of the gut wall, and that part of the body wall which corresponds with it in position and extent. The gut wall always retains its unsegmented character and may lose all relation with the segment by change of position as in the tail region. On the other hand, the muscular part of the body wall undergoes definite changes. There is at first a longitudinal band of muscle fibres extending from end to end of the animal's body. This becomes segmented or broken up into separate pieces of the same length as the sections of the hydrostatic skeleton to which it corresponds and with which it coincides, and the ends of these separate pieces of muscle attach themselves to the circumference of the septa which separate the segments of the hydrostatic skeleton from one another, as shown in fig. 6.

The ectodermal tissues, like the gut wall, are never segmented in this manner, but again like the gut wall, they get their nervous and vascular systems arranged on the segmental plan. This plan is determined by the arrangement of the hydrostatic skeleton and the mesoblastic tissues of the body wall in sections with septa between, which make each section more or less a separate compartment. From the longitudinal blood-vessels and nerve cords branches pass off into each of these compartments for the supply of all the tissues related to the skeleton of each segment. Nephridial organs are also repeated serially in every coelomic cavity for the drainage of these cavities after the manner of excretory organs.

All these structures are called "segmental" because they follow the arrangement of the skeleton which is "segmented," and this of course means that the coelomic space containing the hydrostatic skeleton is also segmented. It must be clearly understood what the difference is between structures that are segmental and those that are segmented. The latter determine the former:

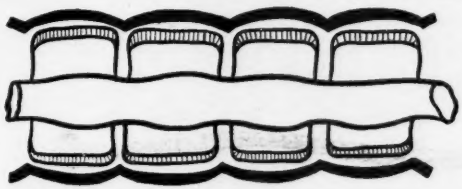

Fig. 6. This shows the attachment of the somatic mesoderm to the boundaries of the coelomic sacs before and behind, and the unsegmented condition of the splanchnic mesoderm. Between the coelomic sacs is a certain amount of blastemal tissue.

that is, the condition of a space controls the arrangement of the animal's tissues and organs.

Before proceeding further, we shall define what is meant when we speak of a mesoblastic segment and a metameric segment.

A *mesoblastic segment* consists of that portion of the mesoderm that is related to one coelomic cavity, and is repeated in every unmodified metameric segment in the body.

A *metameric segment* consists of all the structures of epiblastic, hypoblastic and mesoblastic origin related to one coelomic cavity, and its segmented and segmental structures are repeated serially in every unmodified metameric segment in the body.

The development of the archiannelid Polygordius illustrates the process of segmentation so well that a description of it will be of advantage.

Polygordius is a typically segmented annelid (fig. 7), and its development has been worked out in the greatest detail. Its larva (fig. 8) is free swimming and called a trochophore. This trochophore larva is roughly spherical in shape with an equatorial mouth and a ciliated groove called the prototroch, and a polar anus near another ciliated structure called the telotroch, with an

oesophagus, stomach and intestine extending from the mouth to the anus. The space between the ectoderm and the endoderm is filled with blastemal tissue, and in it are strands of mesoderm with contractile properties passing between the poles of the larva. An archinephridium drains this space. At the upper pole of the larva is a cap of ectoderm with some nervous tissue underlying it and sending out radiating nerves. There is no cavity corresponding to coelomic cavity, so there is no segmentation present in the trochophore larva. Correlated with this, we find the nephridia do not have ciliated funnels, but have instead solenocytes which can drain the blastemal tissue or blastocoele of its body.

When metamorphosis occurs, this larva commences to grow out a tail-like process from its lower hemisphere, which is formed at first of gut tube, ectoderm and blastocoele with its blastomal tissue. This goes on extending until a length of animal is formed, having an anus at the tip of this tail-like structure. This is the body of the animal, and has the same essential parts as the trochophore larva, but these are now disposed in a cylindrical form.

Fig. 7

Fig. 8

Fig. 7. *Polygordius Neapolitanus.* After MacBride[1].
Fig. 8. Larva of *Polygordius* metamorphosing. After MacBride

A later stage shows the mesodermic bands of the larva being continued into the body of the animal owing to the activities of certain mesoderm cells in the region of the lower pole. Two such mesodermic bands are formed and pass into the blastemal tissue of the cylindrical body, one on either side of the gut. The body is now a cylindrical rearrangement of the structures forming the trochophore, and so far shows no sign of segmentation (fig. 9).

The next change in the animal is the appearance of cavities in the mesodermic bands at certain regular intervals, so that there is always a pair at any particular level of the animal. This is the stage of segmentation, and we see only segments of a general mesodermic cavity. The mesoderm itself is still unsegmented, and is lying in the blastocoele having no relation either to ectoderm or gut wall, and a cavity has appeared in it which we call the coelomic cavity, and from its first appearance this cavity is segmented.

[1] *Text-book of Embryology.* Vol. I. (Macmillan and Co. 1914.)

Coincidently with the appearance of these cavities, communications are being established with the exterior, and these communications are going to give rise to nephridia of which one part at least is going to become a nephrostome or ciliated funnel operating in conjunction with these coelomic spaces.

These coelomic cavities go on enlarging until they meet above and below the gut, and come into contact with each other before and behind, forming mesenteries to the gut and also transverse septa from the thinned out walls of the mesodermic bands in which they appeared (fig. 10).

The next stage represents the segmentation of these mesodermic bands into belts, each of which is the extent of the underlying pair of coelomic sacs. The reason for this breaking up of this uniform mesoderm into belts is to allow the body muscle to get attachment and purchase upon the water skeleton as far as possible. The muscle therefore attaches itself as far as it can to the

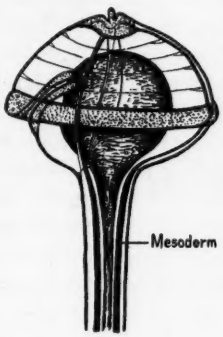

Fig. 9. *Polygordius*: unsegmented mesoderm growing into body. After MacBride.

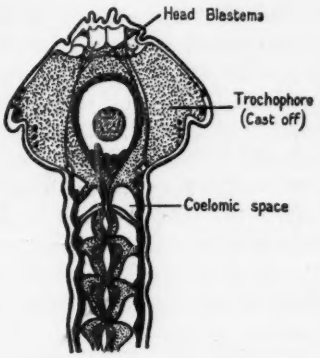

Fig. 10. Mesoderm segmenting. After MacBride.

anterior and posterior boundaries of the sac containing the water or, in other words, to the septa separating coelomic cavities from each other; and in this way, the muscle obtains a hold upon the skeleton, which greatly increases the efficiency of the body muscle. From now onwards, we find this condition always shown as somites in developing coelomate animals of segmented type.

The muscular part of the gut wall is also derived from the unsegmented mesoderm, but this never segments although it has a similar relation to coelomic spaces. The gut tube does not require any improvement upon the movement performed by unsegmented muscle, which condition we find constant in all splanchnic muscle. The hydrostatic skeleton is therefore not related to the gut wall in anything like the manner in which it is related to the body wall, the muscle of which it causes to be segmented in physiological correspondence with its own form.

While this has been going on, changes have been taking place in the trochophore. The stomach is dissolved and the mesodermic bands now retract

the "oesophagus" down to the anterior end of the gut which is in the first trunk segment. Other mesodermic bands, attached to the upper pole of the trochophore, pull this down like a lid upon the first trunk segment. This lid, which consists of the remains of the trochophore, contains the brain and the heart, and its cavity is blastocoele. It contains no gut. All other structures of the trochophore are detached from the animal and disappear. In this way the adult segmented Polygordius comes into being. Its last segment has the anal orifice of the gut, and its first segment has the mouth. The part in front of the first trunk segment is the "face" and is derived from the blastemal tissue of the trochophore covered by ectoderm. It contains the brain or supraoesophagal ganglion and the special vascular organ. There is no coelomic cavity in the face, but there is mesoderm which is observed to remain unsegmented.

After discussing the hydroskeleton of Coelenterate animals we came to the conclusion that it was impossible for any Coelenterate to exist after its removal from the water, as it then lost its skeleton, and with this its form and its ability to move or to procure nourishment to keep it alive. The hydrostatic skeleton has at least overcome this defect, though we shall see that it too is not the ideal skeleton. It is heavy and bulky in proportion to the amount of muscle there is to work upon it; but in the case of an annelid with a hydrostatic skeleton and whose habitat is the sea bottom, being washed ashore and left there by the tide, it could at least live in the littoral or the terrestrial environment, and possibly adapt itself to the new conditions. Indeed something of this kind is supposed to have taken place after coelomates were evolved, in order to account for coelomate animals becoming terrestrial and spreading all over the globe.

3. THE SCLEROTOME SKELETON

Many of these animals, both on land and in the sea, got rid of the water of their bulky hydrostatic skeleton. The direct result of this change was that the place of the hydrostatic skeleton was taken by a skeleton of fibrous tissue. This is the Sclerotome skeleton. It consists of the walls of the coelomic cavities from which the water has been lost; especially the stronger portions formed by the septa separating these cavities, to the margins of which the muscles are already attached.

The sclerotome skeleton is entirely a muscular skeleton. The muscles of the body wall are segmented in correlation with the arrangement of the coelomic cavities, and the muscles depend on this skeleton for their leverage.

The sclerotome skeleton is of great morphological importance, and has allowed of the greatest amount of evolutionary change; but physiologically it is very inefficient. The advantages gained by the loss of water from the skeleton are more than counterbalanced by the disadvantages due to the loss of rigidity. Indeed a rigid skeleton is now the imperative need of the animals

that have arrived at the stage in their evolution when it would be an advantage to get rid of their water skeleton. The evolutionary problem for these animals is how to get rid of their bulky, heavy water skeleton, and acquire a rigid skeleton to supplement the sclerotome skeleton that takes its place. We shall see that this problem has been solved in two distinct and different ways by segmented coelomates. How this has been accomplished we shall now endeavour to illustrate.

The structures that are evolved to supply the rigidity so deficient in the sclerotome skeleton are both formed in connection with ectodermal structures. One is formed in the skin as an exoskeleton, the other is formed from the gut wall to support the dorsal nerve tube, and is a Neural skeleton.

Exoskeleton

One of these acquired rigid structures is the exoskeleton of segmented coelomates. This is formed in the skin of the animal, and is arranged segmentally in correspondence with the segmented form of the particular animal. This is well illustrated in the case of the arthropods. These animals have evolved an exoskeleton which gives the animal the rigidity necessary to maintain its form and also gives additional leverage to the muscles of its body wall. Animals that have acquired a rigid exoskeleton to take the place of incompressible water lost from their coelomic cavities, have probably departed from the line of evolution which leads to the vertebrate form; but they have been able to attain a high degree of specialisation, and a very wide distribution both on land and in the sea. It will be interesting to look at the process involved in this rearrangement of skeletal structures which is illustrated in such an animal as Peripatus.

Peripatus is a typically segmented coelomate which has both annelidan and arthropodan characters, and neither of these characters is typical of either group, as the coelom containing a certain amount of hydrostatic skeleton is much reduced, and the newer exoskeleton is imperfectly formed. Peripatus seems to represent a transitional stage in the evolution of arthropods from annelids.

During its development, which is embryonal and not larval, mesoblastic segments are formed along the sides of the elongated gastrular opening, which is elongated until its sides meet and leave an anterior and posterior opening as primitive mouth and anus. These segments become hollow, and the hollows are coelomic cavities. The coelomic cavities remain small and become filled with water after the manner of annelids generally. Nephridia appear in correspondence with the annelidan plan. The whole body is formed of these segments, so that there is no part anterior to the first segment to which the name "face or preoral part" can be applied. As development proceeds, the anterior segment leaves the gut to assume a preoral position, and a further move in this direction by other segments gives rise to the arthropodan head (fig. 11).

In correlation with this arthropodan form of exoskeleton, the watery

endoskeleton decreases as the exoskeleton increases in amount. This exoskeleton is said to be partly formed of matter which in the annelid is excreted by the nephridia from the spaces containing the skeleton. This exoskeleton is segmental, and its segmental arrangement follows the segmented arrangement of the body. In this way the annelid form may change to the arthropod form

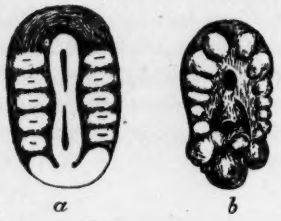

Fig. 11. Two stages in the development of *Peripatus capensis*. The anterior somite in (*a*) is perioral in position, whereas in (*b*) it has moved forward to a preoral position to form the antennary or preoral segment. After MacBride.

of animal, and replace its hydrostatic skeleton with a more rigid, and for many purposes, a more efficient exoskeleton. In all segmented coelomates, the coelom must appear in its primitive condition very early before any segmentation can take place. When this takes place, the coelom may become modified to any degree short of disappearance.

4. THE NEURAL SKELETON

The other acquired structure that supplies rigidity to the segmented coelomate that is dispensing with the water of its endoskeleton is the notochord. This is a neural skeleton, in the sense that it is correlated to the nerve tube on the dorsal surface of the animal. It supports the tube and maintains its tubular form during lateral flexion of the body. As the nerve tube is essentially a non-segmented structure, the notochord, formed primarily for its support, is also unsegmented. It is a solid column of cells that gives rigidity to the animal, but it has no relations to the muscles of the body wall. This is a condition we first meet with in the chordate animals, such as Amphioxus. This animal is developed from a larva which forms its coelom from three pairs of sacs derived directly from the archenteron. The first of these pairs forms a face or preoral part for the animal, and the second pair forms the collar or perioral segment. The third pair of coelomic sacs extends the length of the rest of the body, and the mesoderm of its outer wall becomes segmented in the manner we have seen occurring in the annelids. In the body there is thus formed a large number of coelomic spaces with their myotomes, but these spaces do not contain water. In other words, they have lost their hydrostatic skeleton, and have only retained the rigid parts of the coelomic cavities, to which the segmented muscles are now attached. All the other parts of these spaces break down, and a large coelomic cavity or peritoneum results from these changes. The rigid parts of the walls of the coelomic spaces to which the muscles are attached, form a connective tissue skeleton, and these

inter-muscular septa are called sclerotomes. Each myotome is separated from the adjacent myotomes by a sclerotome or connective tissue skeleton.

The loss of the hydrostatic skeleton has reduced the bulk of the animal to such an extent, that the body of the animal is now no longer cylindrical, but is flattened from side to side. The object aimed at is evidently to attain such a condition as later on in evolution we find in fishes, where the animal can keep itself off the sea-bottom, and move from place to place by the lateral movement of the hinder part of its body. In Amphioxus, the reduction of bulk of the body and its flattening from side to side has also resulted in a loss of leverage for the muscles; and this is added to the fact that the muscles, though strong enough for creeping along the bottom of the sea, are not sufficiently developed for propelling its body through the water away from the bottom.

The fate of all the chordates is that they can never leave the bottom of the sea. Thus in the case of Balanoglossus, the hydrostatic skeleton of the body is replaced by an endoskeleton of thickened basement membranes, which being formed from unsegmented epithelial structures are themselves unsegmented (fig. 12). Segmentation of the body does not exist apart from the collar region,

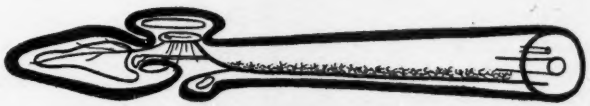

Fig. 12. Diagram of anterior part of Balanoglossus.

and since the mechanics of this form do not meet the requirements, all hope of a free-swimming life is gone. Under these circumstances, Balanoglossus, having a coelomic cavity filled with water in its proboscis, makes of this part a muscular organ for burrowing in the sea-bottom. The cephalochordate Amphioxus retains the segmented structure of the body, but free lateral movement is interfered with by the rigid notochord, which is a new unsegmented skeleton that has been formed and gives support to the new dorsal nerve tube.

In the urochordate animals, where the organisation of structures is in many respects the highest that had at that time been evolved, the mechanical arrangements of the skeleton were so defective that these animals have all given up their freedom of movement with their larval existence, and become sessile and degenerate creatures.

It is probably from a form like Amphioxus that the vertebrate animals have evolved. We saw that when its body lost its hydrostatic skeleton, there were still two great defects which prevented it from being a success as a free-swimming animal. These were:

(1) That its muscles were not powerful enough to keep it away from the bottom.

(2) That they were prevented from acting efficiently by the rigid notochord.

Two great changes mark the transition from non-chordate to chordate characters in animal evolution:

(1) The nervous system which was situated on the ventral aspect of the body now comes to be developed on the surface of the dorsal aspect of the body, and a rigid notochord is formed from the enteron which serves to support it.

(2) The hydrostatic skeleton which occupied the closed coelomic spaces disappears and is replaced by the sclerotome skeleton.

As the notochord persists in the chordates, we have to trace the evolution of the vertebrate endoskeleton in vertebrate animals themselves, as it is here that all the changes occur which transform the notochord into an efficient segmented endoskeleton. This notochord is found in all chordates as an epithelial rod related to the neural tube and acting as a support to it, and, for this reason, we call it the Neural skeleton.

5. THE NEURO-MUSCULAR SKELETON
(Vertebrate endoskeleton)

In the next group of animals—the vertebrates—we find the defects in the structure of the Chordates overcome.

Fishes present us with an enormous increase in the bulk of the muscle in proportion to the size of the skeleton of the animal, so that this defect is readily overcome. The rigidity of the notochord is a more difficult problem.

We have seen that chordates fail very largely on account of this, so do certain chordate fishes, and even the lowest fishes (cyclostomes) try to get rid of the notochord. The anterior end of the notochord begins to break down soon after it is formed, and forms a loose mesenchyme within its sheath. This was observed by Agar in dipnoan fishes, and might be interpreted as an attempt at the removal of the notochord.

This effort at the removal of the notochord does not seem to be satisfactory, probably because by this time the notochord is necessary for the support of the dorsal nerve tube which is developing greatly in this region. The notochord therefore grows again and attains its former length.

As it is found inadvisable to remove the rigid notochord itself, means are taken to overcome its rigidity, and these means can be traced in the formation of a segmental skeleton which is of greater strength, and possesses greater flexibility, in the vertebrate animals. This new skeleton displaces the notochord as a continuous and rigid structure; and in its complete form, is the true segmented vertebrate axial skeleton, or more strictly endoskeleton.

We must now consider the phases presented by different groups of vertebrates, of the formation of a skeleton to take the place of the notochord. The cyclostome fishes present the first effort in this direction. This is very imperfect and consists of little pieces of hyaline cartilage applied to the sheath of the notochord. They are called arcualia because they are the rudiments of arches, which will later attach themselves to the bodies of vertebrae and surround the neural tube.

It is necessary to recall the primitive coelomic conditions to indicate the relations these arcualia bear to that very important structure, or space, the coelom. In all vertebrate animals, the coelomic cavities appear in somites. Each coelomic cavity has an anterior and a posterior wall. The anterior and posterior walls of adjacent cavities are separated from each other by blastemal tissue (fig. 6). The muscle of the myotome is attached by its anterior end to the anterior wall of the coelomic cavity and by its posterior end to the posterior wall of the same coelomic cavity. The ventral root of the spinal nerve gives rise to the motor nerve of each myotome, and this nerve passes direct from the spinal cord to the myotome. The dorsal root of the spinal nerve gives rise to

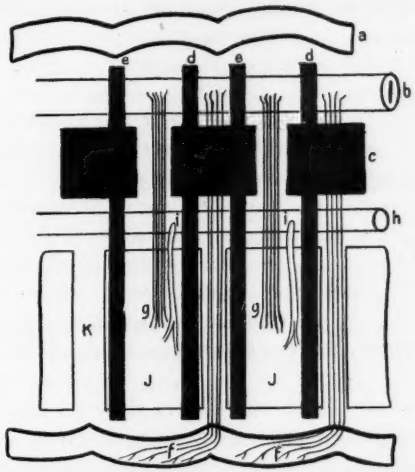

Fig. 13. Diagram of the arrangement of somatic arches in relation to vertebrae and myotomes with segmental arteries and nerves: *a*, skin; *b*, dorsal nerve tube; *c*, vertebral bodies; *d*, anterior neural arches of vertebral relation; *e*, posterior neural arches of vertebral relation; *f*, dorsal or sensory nerves passing in sclerotomes to the skin; *g*, ventral or motor nerves passing to the myotomes; *h*, aorta; *i*, segmental arteries; *j*, myotomes, intervertebral in position; *k*, sclerotomes.

the sensory nerve of the body segment, and this nerve passes between two myotomes to get to the skin of its segment. At this stage the motor and sensory nerves belonging to the same body segment are separated by an interval of the extent of half a myotome, and their roots leave the spinal cord in a like manner, that is a ventral root alternating with a dorsal root, about the extent of half a myotome apart (fig. 13).

The small cartilaginous bodies, or arcualia, which are the beginnings of vertebral arches, appear in relation with the walls of the coelomic cavities, one at the anterior wall and another at the posterior wall. In this manner there are two arcualia formed in relation with each myotome, and these may be called the anterior and the posterior arcualia. When vertebral bodies are formed they do not correspond in position with the myotome. A vertebral

body alternates with a myotome; so that the middle of a vertebral body is placed opposite a sclerotome, which is in the interval between two myotomes, and the nerve of a myotome is opposite an intervertebral space. In the course of development the arcualia pass round the notochord, and then encircle the spinal cord. In this manner they each form a haemal arch and a neural arch. On account of the myotome and the vertebral body alternating with one another, the anterior neural and haemal arches arising in connection with the anterior wall of a myotome, come into relation with the posterior end of a vertebral body when these appear, and the posterior neural and haemal arches come into relation with the anterior part of the vertebral body following. In this way, there are formed two pairs of arches to each vertebra, and these may be called anterior neural and haemal arches respectively (although in relation to myotomes, they would be named in the reverse order).

Recalling the arrangement of the two nerves to each segment as being separate and alternating with one another, it will be evident that the ventral motor nerve and blood-vessel will now pass between posterior and anterior arches of vertebral relation from before backwards, or be intervertebral in position, while the dorsal roots pass between anterior and posterior arches of similar vertebral relation, and are intravertebral in position, so that the motor nerve and blood-vessel pass straight to the muscle from between two vertebrae, while the sensory nerve passes over a vertebra through the space between two myotomes. Thus we have a morphological reason for this double arrangement of arcualia and the separation of sensory and motor nerves in each segment.

As mentioned above, these arcualia are the rudiments of arches and are related to the notochordal sheath, which in cyclostomes is unmodified. These rudiments are related to the notochord so as to form dorsal arcualia which assume a relation to the overlying nerve tube, and ventral arcualia which are the rudiments of the so-called haemal arches. In Myxinidae, these arcualia are extremely rudimentary, and even in Petromyzontidae, they form very imperfect arches, even in relation to the nerve tube.

In cyclostomes we find then, a persistent notochord with additional cartilaginous rudiments developed in relation with the anterior and posterior walls of the coelomic spaces. It is among gnathostomatous fishes that we find the further steps in the evolution of the vertebrate endoskeleton, and we shall proceed to indicate what they are. We now find alterations in the notochordal sheath following upon the presence of the cartilaginous arcualia mentioned. These begin to invade the sheaths of the notochord, and later break up these structures into segments or vertebrae; and from the facts of this process of invasion of the notochordal sheaths by cartilage, we should infer that the vertebral column would be formed after the neural and haemal arches (and this appears to be the case in man), so as to give these arches and the nerve tube increased support. The notochord by itself is probably limited as to the degree to which it is capable of acting as a support in the increasing size of

animal forms, and the notable increase in the amount of nerve tissue. This is expressed by the fact that the notochord sheaths tend to chondrify and to replace the notochord itself, so as to form at first a tube, and later a broken or segmented rod of hyaline cartilage.

In the Dipnoi, we find forms with a notochordal sheath uniformly chondrified. This cartilage is entirely free from segmentation. In other words, segmental form has impressed itself upon the muscles and nerves, but not upon the chondrified notochordal sheath.

The next step appears to be represented by the Holocephali, where the notochord sheath is chondrified in the form of a series of rings, several such rings being formed in each segment of the body. This distribution of cartilage cannot be called segmental. It probably only expresses the manner in which support must be given to a tube containing the notochordal cells under pressure and is a distinct advance, mechanically and functionally, upon the uniformly chondrified sheath mentioned above, as the arrangement allows of a certain degree of flexibility of the notochord.

The anterior arcualia now begin to disappear, and the primitive condition in which two neural arches (anterior and posterior) and two haemal arches (anterior and posterior) were present in each segment, becomes replaced by a condition in which we find only one neural arch and one haemal arch in each segment. This latter condition allows of the ventral nerve and the dorsal nerve of the same segment coming together to form a mixed nerve, an arrangement of the segmental nerve which is adhered to in all the higher vertebrates. These mixed spinal nerves are always accompanied by the segmental blood-vessels.

All vertebrate skeletons above that of Holocephali show secondary segmentation following that of the somatic mesoderm, and the notochordal sheath is modified to form the axial part of the axial skeleton, either by sheath formation or by peri-sheath formation, from the bases of the segmental arcualia. By the time vertebral bodies are being formed, this disappearance of the anterior neural and haemal arches is becoming evident, with the above-mentioned changes in the arrangement of the spinal nerves. The resulting condition for vertebrates generally, is that for each segment there is a corresponding intersegmental vertebra, with one intersegmental neural and haemal arch, while the mixed nerve is now segmental, and myotomic in position.

Having shown that the sclerotome is the skeleton of the myotome, and having pointed out the morphological relation of arcualia to the issuing nerves, it will be evident from the various forms of arcualia among the lower fishes, that such cartilage elements appear primarily in relation to the nerve tube and not to muscle, although they are placed in the intermyotomic intervals or sclerotomes.

In the fishes, where cartilage first appears as an organised skeleton, two facts are to be noted:

(1) The enormous development of muscle.

(2) The slight development of axial skeleton.

The disproportion in amount between these tissues is so great, that it is difficult to believe that any primary relation exists between them.

The true skeleton of the myotome is, as before stated, the sclerotome skeleton, which is always found developed to the extent required by myotomes for their attachment. The sclerotome skeleton is the only structure in fishes that is capable of standing the strain of their powerful muscles. Fishes are the most muscular animals that exist, evolution of muscular tissue having been carried to an extreme degree. This is an adaptation to life in a dense medium: the water they live in absorbs the work of the muscles, and being so dense and difficult to displace, this muscular development is necessary for propelling these animals through this medium.

Passing down the peritoneal aspect of each sclerotome in fishes is a slender rib with its accompanying nerve. It cannot be imagined that such a rib is acting as a skeletal support to the adjacent myotomes, unless to the stratum of fibres of corresponding thickness to the rib. For this purpose the rib would be quite useless, yet the rib being a rigid structure, the muscle attaches itself as far as it can to it and in this way we get an intercostal arrangement of muscles. The rib is, however, really a process of a vertebra and is always accompanied by the segmental nerve. In air-breathing vertebrates, the relation of skeleton to muscle increases. Thus we find in the animals from Amphibia upwards, living generally in a rarer medium than water, that there is again a change, namely,

(1) reduced amount of muscle;

(2) increased amount of skeleton;

both of which are now well specialised.

The muscular relations established in fishes with neural and haemal arches is now exaggerated, so that in higher vertebrates large bones are formed, muscles are relatively reduced and specialised, and their fibrous sclerotomes almost disappear in the adult forms.

This last relation of muscle to skeleton need not be enlarged upon. We are all familiar with the specialised forms of the muscles in the highest vertebrate, and with the way they have taken advantage of almost every particle of the skeleton to give the leverage necessary for the actions of such highly specialised muscles.

In the evolution of the vertebrate skeleton we have seen that archiblastic tissues have the power of providing themselves with a skeleton for protection or support. It is evidently not so with muscle, for we have seen during its whole history, that this tissue had to take advantage of anything it could find to help it to do its work, or to enable it to do it more efficiently. Thus in the coelenterates, the muscle fibres act on the fluid contained in the enteric cavity and that within the bell of the medusa, because it is the only resisting body they can find to act upon. It is for this reason we call this fluid the hydro-skeleton.

In the annelid, the coelomic spaces appear and are full of water. Here the

muscles take advantage of an improved condition, namely, an enclosed mass of water instead of an unenclosed mass, and arrange their attachments according to the changed conditions. Then when transverse septa are formed, they again take advantage of the firm circumferential parts of the septa and attach themselves to them, and in doing so, get broken up into sections which can act more or less independently of one another to the great advantage of the animal.

When the septa of the coelomic cavity disappear, and this no longer contains fluid as in Amphioxus, the muscles retain the circumference of the septa as sclerotomes which serve them as a skeleton until something better is evolved. This next thing is the skeleton which gives support to the nerve tube, and we find the muscles acquiring relations of attachment to this skeleton in fishes. As we ascend in the vertebrate scale these relations are extended until it would appear that they are more important than the relations of the skeleton to nervous system.

The skeleton we have been discussing as the vertebrate skeleton is a neuro-muscular skeleton. It was primarily neural as we have seen, and secondarily muscular; then in its highest form it is neuro-muscular. It forms the skeletal support of the dorsal nervous system. It is also the skeleton of the somatic muscles, and it is segmented in conformity with the body segmentation.

The neuro-muscular skeleton is, as we have seen, formed round the notochord which is a structure of hypoblastic origin. This is therefore unsegmented, and it is entirely superseded by the neuro-muscular skeleton, and almost entirely removed by it. The neuro-muscular skeleton may therefore be described as of mesoblastic origin, not only being formed from mesoblastic tissue, but its structure being determined by the arrangement of the mesoblastic somites, which in turn were determined by the arrangement of the coelomic cavities. In other words, it arose as an extension of the sclerotome skeleton which remained after the disappearance of the hydrostatic skeleton, and is therefore the result of mesoblastic segmentation depending upon the segmentation of coelomic cavities.

ODONTOLOGICAL ESSAYS

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FIRST ESSAY

ON THE DEVELOPMENT OF THE PALATE AND ALVEOLAR RIDGE IN MAN

It seems desirable, not to say necessary, as a general introduction to the following essays, to record briefly the results of my researches upon the development of the palate, tooth-band and alveolar ridge in man. The communication of these results is justified by the consideration that it brings out some ontogenetical principles, which will find their application in the following essays, and further that it shows that some of the readings of the development of this part of the human mouth which are adopted in textbooks of Embryology are not entirely true.

Upon the earliest stages of the development of the human palate until the complete separation of cavum oris and cavum nasi by the coalescence of the two palatine processes, I have nothing to say; the purpose of this essay is to elucidate the developmental phenomena in the palate after the uniting of the processus palatinus in the middle-line.

The starting-point of our research is the palate of a fetus of five months, the oral surface of which is outlined in fig. 1. One may distinguish two regions in this palate, a central part and a surrounding border. I denominate the first *Tectum oris*, the second, *Zona marginalis*.

The tectum oris is egg-shaped, and is continued backwards as the soft palate, of which the outline is lacking in this figure. The tectum oris as a whole is concavely vaulted, its lateral parts are in this stage of development, but slightly prominent. I will distinguish these prominences as *Tectal ridges*. Between the tectal ridges and the zona marginalis there runs an uninterrupted furrow. The surface of the tectum oris is still characterised by a number of well marked rugae palatinae, extending from the middle-line, to the groove separating the tectal ridges from the zona marginalis. This fact is of some importance in regard to the interpretation of the anatomical conditions in earlier stages.

In its foremost part the median line of the tectum oris is occupied by the papilla palatina which is connected with the papilla labii superioris by a fold of the mucous membrane, which will be distinguished as the *Fraenum tecto-labiale*.

The zona marginalis is horseshoe-shaped, and surrounds the tectum oris.

In the front part of the mouth it lies between the latter and the lip, laterally between the cheeks and the tectum. It is separated from lips and cheeks by a rather deep furrow—the vestibular groove—interrupted in the median line by the fraenum already referred to. The internal boundary line of the zona marginalis is a somewhat more complicated one. A furrow, which separates the zona from the tectum, begins at the fraenum tecto-labiale and deepens as it passes outward and backward. A little behind the mouth this furrow turns obliquely outward, finally fusing with the vestibular groove. Thus the zona marginalis is divided into an anterior and a posterior part. The latter is separated from the tectum oris by a special furrow which is apparently a backward prolongation from the furrow in the front part of the palate. On grounds, which will become intelligible in the course of this essay, I shall distinguish the first furrow—that ending the vestibular groove—as the *internal alveolar furrow*, that limitating the posterior part of the zona marginalis on the inner side as the *transitory palatine furrow*.

The posterior part of the internal alveolar furrow divides the zona marginalis into two parts, whose significance in the future development of the palate is quite different. For the anterior part is the alveolar ridge, in this phase but partially developed, whereas the posterior part has nothing to do with this ridge; being, as development advances, incorporated in the tectum oris by the disappearance of the transitory palatine furrow. This fusion with the tectum is as a rule already complete when the fetus is full grown: so that in the new-born child only some small fragments of the furrow persist on the inner side of the alveolar ridge, which by this time has extended considerably further backward. The different signification and behaviour of the two parts of the zona marginalis necessitate the application of a special name to each; the anterior part, as the true alveolar ridge, shall retain that name, the name *pseudo-alveolar ridge* being appropriate to the posterior part in the light of its later development. In fetuses, more advanced in development than that of fig. 1, the alveolar ridge has penetrated between the cheek and the pseudo-alveolar ridge.

The surface of the pseudo-alveolar ridge is smooth, that of the alveolar on the contrary is rugged; small irregular prominences indicating the spots where the teeth are lying under the surface of the gum.

In a fetus in an earlier stage of development, anatomical conditions are met with, which prove that the above described configuration of the palate does not originate by a simple enlargement, but by a development of very particular nature. This becomes obvious by a comparison of fig. 1 with fig. 2, in which the palate of a fetus from the fourth month is outlined.

The most striking difference between the palate sketched in fig. 1 and that of the younger subject drawn in fig. 2, is that in the earlier stage the zona marginalis is incomplete, being represented only by its anterior and posterior extremities. The anterior part, the alveolar ridge, is narrower and sickle-shaped, lying between the lips and the tectum oris. The corrugations by which it is

characterised in the older fetus have not appeared, its surface being smooth. In the median line it is divided into two halves by the Fraenum tecto-labiale. The papilla palatina and papilla labii superioris lie closer to one another, and are connected by the short and broad Fraenum. A little behind the corner of the mouth the internal alveolar furrow and the vestibular furrow unite, forming a common groove, which runs backwards between the cheek and the tectum oris. Examination of the rugae palatinae makes it clear, that the tectum oris in this stage extends laterally as far as the cheeks, for the rugae reach these lateral walls of the mouth. In this region therefore the zona marginalis is lacking. In the most posterior part of the palate it reappears, the pseudo-alveolar ridge intercalating itself between the cheek and the tectum oris, being bounded internally by the transitory palatine furrow, and externally by the vestibular groove.

Summarising, one finds that in a younger stage of development the zona marginalis is wanting in part, and the tectum oris extends laterally as far as

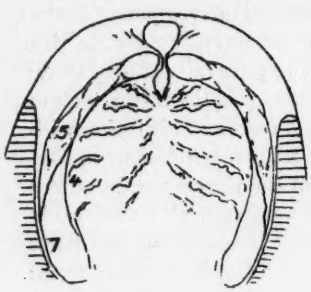


Fig. 1

Fig. 2

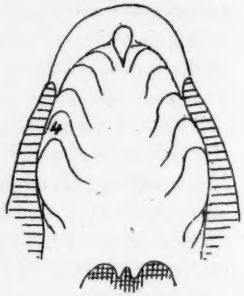


Fig. 3

the cheeks. Moreover the lateral parts of the tectum project more considerably, and the palate is therefore more strongly vaulted from side to side.

Knowledge of the structure at this stage of development facilitates the understanding of the conditions in a still earlier stage, drawn in fig. 3. This is characterised by the total absence of the zona marginalis, the palate being represented in this subject solely by the tectum oris. In the front part of the mouth the latter reaches the lips; laterally along its whole length it touches the cheeks. That such is really the case is proved by the fact, that the rugae palatinae on the front part of the palate reach the furrow bounding the lip, and posteriorly extend outwards to the groove between the cheeks and the palate. If the lateral groove in this stage is called the vestibular groove, stress must be laid on the fact that its anatomical value is not the same as the vestibular groove in the stage represented in fig. 1. The conditions in the two subjects are quite different. For in the elder stage this groove runs between the zona marginalis and the cheeks and lip, whilst in the younger it separates these from the tectum oris. Therefore it is advisable to distinguish the groove in

the latter case by a special name at the labio-tectal and bucco-tectal furrow. The total absence of the zona marginalis in fig. 3 involves lack of the internal alveolar furrow and the transitory palatine furrow.

A very remarkable phenomenon is presented by the eminence lying in the front part of the palate. In older stages two papillae are situated in the median line: a papilla palatina and a papilla labii superioris, which are connected with each other by the Fraenum tecto-labiale. In the present case both papillae are represented by a single egg-shaped eminence, the Fraenum being still undeveloped.

The three stages of development above described, enable us to explain the history of the differentiation of the human palate after the fusion of the two palatinal processes. I wish to emphasise the fact that this description applies only to the development of the palate in man, and must not be extended to other mammals. I am aware of the circumstance that the developmental history of this part of the mouth in some other mammals differs not inconsiderably from that in man, especially so far as it concerns the alveolar ridge. In the following paragraphs I will try to give a short summary of this history.

The so-called secondary palate is formed by the fusion in the middle line of the left and right palatine processes, the resulting plate separating the primitive cavum oris into an upper and a lower cavity. This secondary palate is in man transitory, representing only that part of the definitive palate which lies within the alveolar ridge. It is thus not identical with the final palate, which includes this ridge and may therefore be distinguished as the *tertiary palate*.

The secondary palate is strongly vaulted from side to side, the lateral parts forming two prominences, along the inner surface of the cheeks, from which they are separated by the labio-bucco-tectal furrow. In the median line this furrow is interrupted by a rather large papilla: the labio-tectal papilla. The two prominences, just referred to, may be distinguished as *tectal ridges*.

The tertiary palate arises from this by the growing up of a ridge, which originates from the bottom of the labio-bucco-tectal furrow, and sandwiches itself between the tectal ridges on the inner side, and the lip and cheeks on the outer side. This ridge embraces the secondary palate like a horse-shoe. Two divisions of the palate so constituted are to be distinguished: a central part—the true roof of the mouth—tectum oris, and a border, the zona marginalis which surrounds it. This zona originates in each half of the palate from two centres, an anterior and a posterior one. The latter becomes visible before the former. The anterior part of the zona makes its first appearance at the surface immediately laterally to the tecto-labial papilla, and extends gradually backwards to touch the posterior part. The two parts however do not unite with each other as a rather deep furrow remains between them after their contact. This furrow is the continuation of that between the tectum oris and the frontal part of the zona marginalis.

The two parts of the zona have different relation to the set of teeth, and it

is therefore necessary to give them different names, the anterior part I call the alveolar ridge, whilst the posterior part may be distinguished as the pseudo-alveolar ridge. The former is bounded by the vestibular groove and the internal alveolar furrow, the latter by the vestibular groove and the transitory palatine furrow.

The surface of the alveolar ridge shows some prominences, caused by the developing teeth, the pseudo-alveolar ridge on the contrary remains smooth and flattens gradually as the transitory palatine groove disappears. At birth, therefore, the limits of this part of the zona marginalis are difficult to determine. The main cause of this difficulty is the backward extension of the alveolar ridge which insinuates itself between the cheek and the pseudo-alveolar ridge, so as to give that prominence an internal position, where, on the total disappearance of the transitory palatine furrow it becomes fused with the tectum oris. In an early stage of development the foremost part of this median line of the palate is interrupted by a small eminence, the papilla tecto-labialis. In consequence of the growing up of the alveolar ridge between the lip and the tectum, this papilla is divided into an anterior labial papilla and a posterior tectal papilla, united by a mucous fold, the Fraenum tecto-labiale. Till shortly before birth the presence of this fraenum is easy to demonstrate. After birth this fold is partly flattened by the gradually accentuated prominence of the alveolar ridge, and only the anterior part—known as the Fraenum labii superioris—persists. In some Prosimiae (Lemur, e.g.) the whole Fraenum is persistent, running between the two central incisors from the lip to the palate. It seems to me not impossible that the diastema sometimes occurring in man in the median line of the set of teeth is caused by the persistence of this fraenum during a longer period than usual.

I have controlled and completed this developmental history of the human palate based on its surface anatomy in fetuses of different ages by the microscopical researches with which the following account deals. It is obvious that the value and significance of such a microscopical investigation are greater ones than those of a purely macroscopical study. For this research ought also to include the genetical and topographical phenomena concerning the teeth and the dental lamina and their relation to the superficial furrows above described.

I have examined by means of serial sections a large number of human fetuses with regard to the anlage and further development of teeth and palate, from these I choose for description five specimens varying in age from the second till the fifth month of development. The youngest embryo measured 25 mm. whole length.

I begin with this embryo, which is represented in figs. 4–7. As shown by these figures in this embryo the separation between the cavum oris and the cavum nasi is not yet formed, the palatine processes still lying lateral and ventral to the dorsum of the tongue. Figs. 6 and 7 are drawn from transverse sections behind the corner of the mouth, figs. 4 and 5 from similar sections in

front of this corner. In this embryo there is not the minutest trace of the teeth-germs. In figs. 4–7, as well as in all those which follow, the interesting epithelial formations are indicated by dotting. In fig. 4 one sees nearly in the middle of the surface of the common anlage for lip and palate a shallow furrow (fig. 4, 1) which may be distinguished as the labio-tectal furrow. Below, with this furrow an epithelial thickening has grown into the subjacent tissue, which shows two offshoots, a medial and a lateral one. I shall call the medial the dento-gingival sheet (fig. 4, 2) and the lateral the labio-gingival sheet (fig. 4, 3). These names indicate the future significance of these epithelial formations; from the former are differentiated the enamel-organs of the teeth, whilst in addition a part of the gum takes origin from it; the latter gives rise to the epithelium on the inner surface of the lip and furthermore to a part of the gum. I lay stress upon the fact that neither of these sheets is distinguished by me as dental lamina, being convinced that such a name is too restricted, as I shall show in the course of the present paper.

The two epithelial sheets above described separate three ridges of mesenchyme. Of these the medial one will be called the tectal ridge (fig. 4, 4),

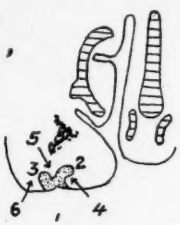


Fig. 4

Fig. 5

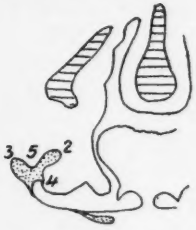


Fig. 6

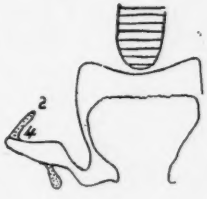


Fig. 7

in the later parts of this paper, the middle the alveolar ridge (fig. 4, 5) and the lateral one the labial ridge (fig. 4, 6). The appropriateness of these names will be shown by the behaviour of the ridges in later embryos.

The conditions of these ridges do not alter much as they are traced backward through the serial sections until at a point a little in advance of the corner of the mouth, the labio-gingival sheet disappears and the common epithelial mass is carried inward only by the dento-gingival sheet, which is slightly inclined medially (fig. 5). That this is a normal structure and not an individual peculiarity of the embryo is shown by conditions in later stages. The region where the labio-gingival sheet is absent is short because it reappears immediately behind the corner of the mouth (see fig. 6).

As this region is in the cheek the name labio-gingival must be replaced by bucco-gingival. The whole epithelial formation in this region arises from the surface epithelium forming the lateral border of the cavum oris, the labio-tectal furrow has disappeared, and the groove between the tectal ridge (fig. 6, 4) and the cheek may be distinguished as the bucco-tectal groove.

Further back the bucco-gingival sheet becomes lower and finally disappears

(fig. 7) and the dento-gingival sheet above is continued to the posterior part of the mouth where it disappears.

The conditions in a fetus of 40 mm. are shown in figs. 8, 9, 10 and 11. The cavum oris in this specimen is separated from the cavum nasi, the secondary palate is complete and the germs of all the milk teeth are present. In fig. 8 a section is drawn between the germ of the lateral incisor and the canine tooth, nearly the same level as the section drawn in fig. 4 of the younger embryo. The changes which have taken place may be recognised in the easiest manner by a comparison of the two figures.

Fig. 8

Fig. 9

Fig. 10

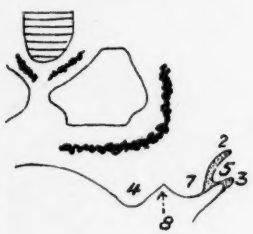


Fig. 11

The labio-tectal furrow has deepened, so that the lip becomes more prominent and acquires a free inner surface. A considerable heaping up of epithelium separates the labial ridge (6) from the tectal ridge (4) and from this common epithelial strand the dento-gingival sheet (2) goes out in a mesial direction, whilst the labio-gingival sheet is directed upwards and laterally. By the considerable elongation of both sheets the alveolar ridge is much broadened.

The section represented in fig. 9 runs through the germ of the canine tooth; at this level the upper and lower lip are united with each other. This section corresponds nearly with that in fig. 5.

There is a rather broad bucco-tectal cleft and between the cheek and tectal ridge (4) is intercalated the backward prolongation of that large epithelial

mass, which in the preceding figure is shown to separate the tectal and labial ridges. In the present section as in that of fig. 5 there is but a single offshoot going out from this thickening of the surface epithelium, namely the mesially inclined dento-gingival sheet (2), carrying at its free edge the germ of the canine tooth. As in the younger fetus the bucco-gingival sheet is absent in the region of this tooth. Hence a lateral limitation of the alveolar ridge (5) is lacking in this region.

A little further backwards this sheet reappears, as is shown by fig. 10, which section runs through the germ of the first milk molar. The cleft between the cheek and the tectal ridge is deepened and widened out. This bucco-tectal groove cannot be identified with the vestibulum oris, for the vestibular cavity is not in existence in the present stage of development. The cleft between the cheek and the tectum oris is only of short duration, it disappears in the course of the further development, as will be demonstrated in older embryos.

The section drawn in fig. 10 is taken through nearly the same region as that of the younger embryo which is the original of fig. 6. It shows a new feature which is worthy of special notice. This is that the dento-gingival sheet no longer arises from the lateral edge of the tectal ridge (4) but originates more laterally. Fig. 11, which represents a section through the posterior part of the palate, shows that this condition is accentuated as the structures are followed backward. In it the bucco-gingival sheet (3) has become very low, penetrating only a little way into the subjacent tissue. The dento-gingival sheet (2) has still a considerable depth. On the surface of the palate the tectal ridge (4) is much flattened, and the tecto-buccal cleft, although considerably broadened, has become very shallow. Between the cheek and the tectal ridge a new ridge is formed (7) which has nothing to do with the alveolar ridge (5). For the dento-gingival sheet extends laterally from this new formation. The ridge in question is that described by me earlier in this paper as pseudo-alveolar ridge, it is separated from the tectal ridge (4) by the shallow furrow which I have distinguished as the transitory palatine furrow (8).

I choose an embryo of the age of two and a half months as a third stage. The figs. 12, 13, 14 and 15 are drawn from it.

The section in fig. 12 cuts the germ of the lateral incisor, and corresponds therefore with those in figs. 4 and 8. There is an enormous heaping up of epithelium between the tectal ridge (4) and the labial ridge (6). By this considerable thickening of the epithelium these ridges are pushed away from each other and in consequence the alveolar ridge (5) is broadened. By the penetration of the labio-tectal furrow into this mass of epithelial cells the lip becomes more and more independent and acquires a free inner surface.

The deepening of this furrow is due to an atrophy of the cells which fill the interior of the epithelial mass. The dento-gingival sheet (2) is strongly inclined mesially, so as to take nearly a horizontal direction. The labio-gingival sheet (3) bounding the alveolar ridge (5) along its lateral edge, is also thickened and penetrates more deeply into the mesenchyme.

The section drawn in fig. 13 cuts through the enamel organ of the canine, being therefore comparable with figs. 9 and 5. This section lies behind the corner of the mouth. At this level there is, more anteriorly, a considerable thickening of the epithelium between the cheek and the tectal ridge (4), pushing these parts away from each other. From the medial upper edge of this epithelial mass, the dento-gingival sheet arises, terminating in the germ of the canine. Lateral of this lamina extends the alveolar ridge (5), which is continuous with the mesenchyme of the cheek, because in this embryo, as in the two already described, the bucco-gingival sheet is wanting at this level. The bucco-tectal cleft is widened and deepened, owing to the atrophy of the superficial cells.

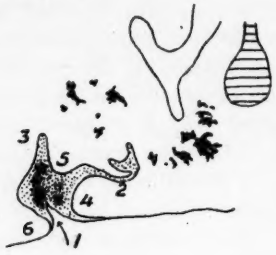


Fig. 12

Fig. 13

Fig. 14

Fig. 15

Further back the dento-gingival sheet shows the same behaviour as in the earlier embryo. It no longer takes origin from the medial upper edge of the common epithelial mass, but it is pushed laterally, approaching the bucco-gingival sheet, which has reappeared at this level, as demonstrated by fig. 14, passing through the posterior part of the enamel-organs of the first milk molar. By this change of position the alveolar ridge (5) becomes thinner, and medial of it, the pseudo-alveolar ridge (7) appears, its surface covered by a thick epithelial layer. This layer forms the bottom of the bucco-tectal cavity, which is very broad and in consequence of the strong projection of the tectal ridge also very deep.

Further back the conditions change gradually in the following manner (fig. 15). The dento-gingival sheet gradually moves laterally, coming at first into relation to and finally fusing with the bucco-gingival sheet. From this

point the dento-gingival sheet forms the dividing band between the cheek and the palate. By the shifting of the dento-gingival sheet, and its fusion with the bucco-gingival, the alveolar ridge gradually disappears, whilst the pseudo-alveolar ridge develops and broadens. By the flattening of the bucco-tectal groove it finally appears on the surface, being covered with a thin layer of epithelium. The section shown in fig. 15 cuts through the enamel-organ of the second milk molar. And it is obvious that in this region the alveolar ridge has not yet developed. The specimen from which the sections outlined in figs. 12–15 are taken, was nearly in the same stage of development as that whose palate is represented in fig. 2. And a comparison, specially of the figs. 14 and 15 with

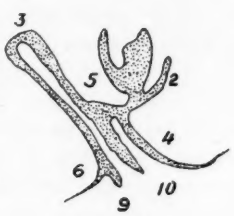


Fig. 16

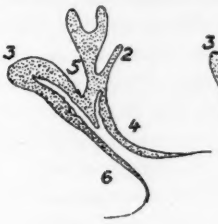


Fig. 17

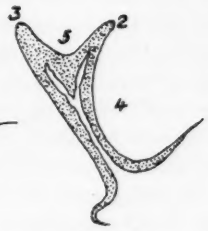


Fig. 18

Fig. 19

Fig. 20

Fig. 21

fig. 2 will greatly facilitate an understanding of these developmental conditions.

Figs. 16 to 21 represent six sections from a series of an embryo at the end of the fourth month. This stage of development is characterised by the final separation of lip and palate, and the ingrowth between these of the alveolar ridge.

The section drawn in fig. 16 cuts through the enamel-organ of the lateral incisor. Comparison of this section with fig. 12 will give a clear idea of the changes which have happened in the interval between these two embryos. The changes are very considerable. In the stage, prior to the present, a cleft was formed in the epithelial mass between the lip and the tectal ridge. Now in this older stage, this cleft not only has broadened but is also complicated

in a typical manner. It is duplicated, or, more exactly, in penetrating more deeply the epithelial mass, it has bifurcated into a lateral and a medial cleft. This enlargement of the groove is due principally to an outgrowth of the epithelial lamina into the mesenchyme, joined with an atrophy and loosening of their interior cells.

The lateral cleft, having pushed into the labio-gingival sheet (3) to its upper extremity, the lip has become fully free, whilst the alveolar ridge has acquired a free outer surface. This lateral cleft is therefore in its deeper part the true vestibular groove (9), for it separates the lip and the alveolar ridge (5) from each other. The latter however, as clearly shown by fig. 16, does not yet reach the surface, it remains under the level of tectum oris and lip.

The epithelial mass building up the labio-gingival lamina is, as now stated, divided into two layers, one lining the oral surface of the lip, the other lining the gum on the outer surface of the alveolar ridge. This behaviour justifies our denomination: "labio-gingival sheet."

The medial cleft (10) penetrates less deeply than the lateral and is inclined to the base of the dento-gingival sheet but without pushing into the latter. In the foregoing description of the surface anatomy of the palate in human embryos, I distinguished this cleft as internal alveolar furrow. Between this and the vestibular groove there is situated a cup-shaped investment of epithelium cells upon the alveolar ridge, which reaches the surface between the lip (6) and the tectal ridge (4). In fig. 2 this mass is seen on both sides of the tecto-labial papilla. The section in fig. 16 demonstrates clearly that in the frontal part of the mouth the alveolar ridge (5) gets its free labial surface before its palatinal, for in this stage the dento-gingival sheet is still solid, being not yet hollowed out.

The elucidation of the present section renders the following easier to understand. In fig. 17 a section through the germ of the canine is outlined. As the tectal ridge (4) is here nearly in contact with the lip, a very narrow but deep tecto-labial groove is formed. This groove bifurcates and the lateral continuation penetrates into the labio-gingival sheet. This is the vestibular groove, whilst the mesial continuation—the internal alveolar furrow—pushes into the dento-gingival sheet, as far as the neck of the enamel-organ of the canine. This section proves that the dento-gingival sheet (2) is partly hollowed out by atrophy and loosening of its interior cells, the remainder forming the epithelial layer covering the inner surface of the alveolar ridge (5).

This process becomes yet more evident in sections a little further back in the spatium interdentale between the canine and the first milk molar, as shown in fig. 18. The great prominence of the tectal ridge (4) in the region in question forms a very deep but narrow bucco-tectal groove, branching out at its extremity into a short vestibular groove, pushed into the bucco-gingival sheet (3), and a similar short internal alveolar furrow penetrating the dento-gingival sheet (2). The alveolar ridge is already well shewn at this level, as a broad prominence between the cheek and the tectal ridge (4).

In the region of the first milk molar the condition becomes more complicated by the appearance of the pseudo-alveolar ridge. Fig. 19 gives an outline of a section cutting through the enamel-organ of this molar. The bucco-tectal cleft has widened, acquiring a broad roof. This roof shows two prominences: a larger lateral and a smaller medial one. The lateral prominence is the alveolar ridge (5) covered by a thick layer of epithelial cells, and bounded by the vestibular groove (9) as a lateral continuation of the bucco-tectal cleft, and the internal alveolar furrow (10). The lower medial prominence is the pseudo-alveolar ridge (7). It must be noticed that the line of attachment of the dento-gingival sheet (2) to the covering epithelial layer corresponds with the internal alveolar furrow, and that the pseudo-alveolar ridge (7) is introducing itself as a new formation between the tectal ridge (4) and the alveolar ridge (5).

The latter condition is demonstrated yet more obviously in the section through the enamel-organ of the second milk molar, outlined in fig. 20. The tectal ridge (4) has moved considerably from the cheek, the bucco-tectal cleft becoming in consequence a widely opened shallow cavity with an irregular bottom, showing two eminences. The medial one is the much broadened pseudo-alveolar ridge (7), the lateral one is the alveolar ridge (5). In a bucco-lingual direction the following furrows are cut in the bottom of this cavity: the vestibular groove (9), the internal alveolar furrow (10) and, finally, the transitory palatine furrow. The second again corresponds with the line of attachment of the dento-gingival sheet (2) to the superficial epithelium.

This section proves in a conclusive manner the fact that the pseudo-alveolar ridge (7) cannot be a formation which later enters into relation to the set of teeth. For if such was really the case, the second as well as the first molar, would, in the course of their further development have to perforate the dento-gingival sheet. And we know that the enamel-organs of all teeth develop lateral of this lamina.

The reduction of the alveolar and the increase of the pseudo-alveolar ridge continue backwards, till at last, behind the gum of the second milk molar, the former has totally disappeared, and the bottom of the cavity between the tectal ridge and the cheek is formed only by the vaulting of the pseudo-alveolar ridge as is shown by fig. 21. In this region the dento-gingival sheet is shifted laterally as far as possible.

To get an idea of the developmental phenomena in this hindmost part of the palate, one may compare fig. 19 with fig. 14, and the figs. 20 and 21 with fig. 15. From this comparison one learns that the anatomical conditions in fig. 15—representing a section through the second milk molar in a younger embryo—are very likely those in fig. 21, giving a section behind the second milk molar in an older embryo. Also the comparison of fig. 15 with fig. 20 is very instructive. Both sections cut through the enamel-organ of the second milk molar. But in the younger specimen (fig. 15) there is not yet a vestige of an alveolar ridge lateral to the dento-gingival sheet (2), in the older embryo;

on the contrary, it is already well developed in this region. Hence, it follows that the alveolar ridge elongates during the development.

Thus the present embryo demonstrates in an unquestionable manner that the alveolar ridge of man is a quite new formation taking its origin in the gap between the secondary palate and the surrounding soft parts: lip and cheeks, in fact that this ridge is not a differentiation of an external border of the secondary palate. In detail the origin of this ridge differs slightly in its anterior and posterior part, but the main outlines are uniform throughout.

Finally, I give in the figs. 22, 23 and 24 three sketches of sections of an embryo of five months. In fig. 23 a section is reproduced going through the lateral incisor. To get an idea of the developmental changes which have occurred in this region one has to compare this figure with fig. 16. The most striking change relates to the alveolar ridge. In the younger stage, sketched in fig. 16, this ridge did not yet reach as far as the surface, it was but of a minute development, lying in the gap between the lip (6) and the tectal ridge (4)

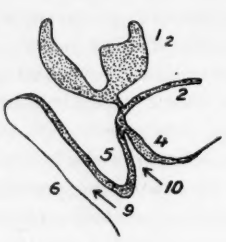


Fig. 22

Fig. 23

Fig. 24

and only its lateral side had a free surface. In the older embryo this ridge has considerably developed, the thick layer of epithelium cells, which covered it, is thrown off, and it has grown out so strongly between the lip and the tectal ridge, that it has pushed these two formations entirely away from each other. It now even projects a little above the tectal ridge (4). The vestibular cleft (9) as well as the internal alveolar furrow (10) have deepened and widened, so that the alveolar ridge has now a free internal surface. The deepening of the latter furrow is achieved by the atrophy and throwing off of the internal cells of the dento-gingival sheet. This is proved by the fact that in this stage of development the neck of the enamel-organ of the second incisor is attached to the oral epithelium in the internal alveolar furrow, whilst originally this organ was attached to the dento-gingival sheet, quite at its free edge, as shown by fig. 12. On comparing the latter figure with fig. 22, it becomes evident that the internal alveolar furrow has penetrated into the dento-gingival sheet, as far as the spot where the germ of the incisor takes origin. Therefore the so-called dental lamina of authors—a term intentionally not

used by me—is an epithelial band, which forms not only the germs of the teeth, but also the gum on the inner surface of the alveolar ridge. After comparing fig. 12 with fig. 22 there cannot remain the least doubt upon this fact. Hence my distinguishing of this band as dento-gingival sheet.

Fig. 23 is a drawing of a section through the germ of the canine. This figure should be compared with fig. 17, showing a section through the same tooth in a younger embryo. The differences between these sections are in the main identical with those in the front part of the mouth. In the older stage the alveolar ridge (5) nearly fills up the cleft between the tectal ridge (4) and the cheek, its internal surface has become free by the hollowing out of the dento-gingival sheet, as far as the neck of the enamel-organ of the canine. For the rest this figure asks no further explanation.

Finally, fig. 24 shews a section of the same embryo, going through the enamel-organ of the first milk molar. This figure is to be compared with fig. 19. Such a comparison shows that the tectal ridge (4) in the older embryo has relatively increased in size; the cavity between the cheek and the alveolar ridge, originally deep and narrow, is now very wide and shallow, the bottom of it is formed by the broad pseudo-alveolar ridge (7) and the also broadened alveolar ridge. This bottom is incised by three furrows: the transitory palatine furrow (8) between the tectal and the pseudo-alveolar ridge; the internal alveolar furrow (10) between the alveolar and pseudo-alveolar ridge, and the vestibular groove in its well-known situation.

After the description of the five stages of development now given, it is very easy to reproduce by means of some simple diagrams the main features in the developmental history of the human palate, specially the origin of the alveolar ridge and its genetical relation to the epithelial formations growing into the mesenchymatous tissue of the palate. Before doing so, it seems necessary to me to remark, that I have never met in human embryos with the considerable heaping up of epithelium extending along the length of the jaw, distinguished as "Zahnwall" by the German authors. I have had under observation a large number of serial sections of the mouth of human embryos. But, as shown by figs. 5 and 6, even in the youngest stage there is no trace of an outward thickening of the epithelium. On the contrary, from the outset, the surface of the jaw shows a shallow furrow, marking the position of the ingrowing epithelium. In this matter I agree with Leche, that this heaping up of epithelium does not represent an occurrence typical of all mammals. At all events it does not occur in man.

In fig. 25 five diagrams are reproduced, showing the manner in which in man the alveolar ridge develops, and also the origin of the gums. I specially lay stress upon the fact that this ridge is a new formation, and that the gums are differentiated in consequence of a splitting of a primitively solid epithelial lamina. For the rest the diagrams don't need any special explanation; to the reader who has taken cognizance of the preceding descriptions they are undoubtedly sufficiently intelligible.

Finally, the question as to the significance of the pseudo-alveolar ridges must be considered. These organs which in a young stage form the very prominent posterior half of the zona marginalis on both sides of the palate, are, as already sufficiently indicated, transitory. In the older stages they are surrounded by the alveolar ridges, prolongating backwards, and become incorporated in the central part of the palate, which I distinguished as tectum oris. To solve the question of their significance seems to me a rather difficult matter. Klatch, after having confirmed the occurrence of these organs first described by me in human embryos, is perhaps right, when he considers them as rudimentary organs, inherited by us from our marsupial ancestors, where they may have assisted the young in holding on to the nipple.

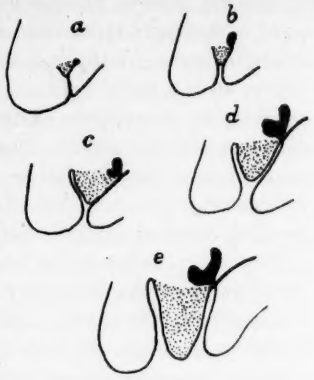


Fig. 25

SECOND ESSAY

ON THE DEVELOPMENT OF THE ENAMEL-GERM

To write a special essay upon the development of the enamel-germ, worth reading, may seem a somewhat bold endeavour. For the development of this part of the tooth-germ has already so often been the subject of investigations, that it may be considered as improbable that particularities of some importance are as yet unknown. However, at the very outset of this essay it must be said that the descriptions of the development of the enamel-germ as given in the textbooks of Anatomy or Embryology are incomplete.

So simple a matter as the development and internal structure of the enamel-germ is without exception described in an incomplete manner. This is the case not only in the textbooks written in English, but also those written in German and French. And often during my researches upon this subject, I have wondered at the fact, that phenomena so simple and appearances so easily observable as those described in the present paper, are still unknown. For the facts referred to occur with such a regularity and are so unmistakable, that they may easily be verified by anyone desirous to do so. But a prime requisite for such a study is the examination of complete serial sections of several subjects of different ages. Only in this way does it become possible to survey the relation between the changes in the succeeding stages, and to build up the complete history of the development of the enamel-organ.

Not without intention, at the outset of this essay, I lay stress upon the value of the facts to be described hereafter, for they are of primary significance

as a starting point to the dental theory which will be gradually developed in the succeeding essays. In saying so, I remember, that in my own mind, the first conception of the principles of this theory was founded on observations of some phenomena during the development of the enamel-organ in embryos of man and monkeys.

The facts to be dealt with in the present paper, possess therefore a double signification: as ontogenetic phenomena and as the principal elements of a theoretical construction. In this latter significance they can only be utilised later on, in connection with facts and meanings, worked out in succeeding essays. Therefore in the present communication, I confine myself to the facts alone.

The first principal fact which I intend to demonstrate in the present essay is as follows: enamel-organs are, during a certain phase of their development, connected with the tooth-band or dental lamina by means of *two* strands, a

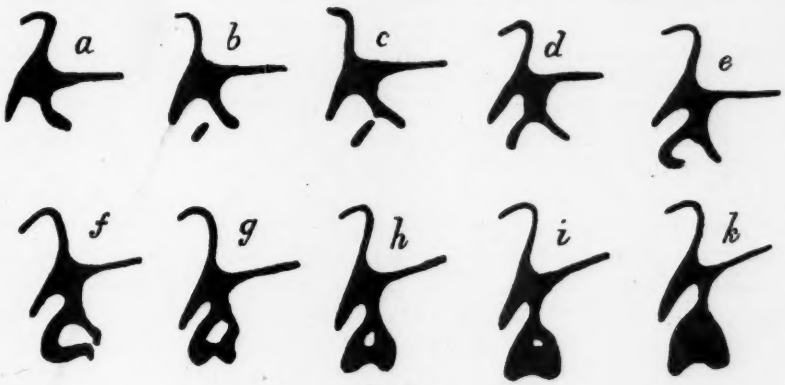


Fig. 26

lateral and a medial one. The large number of embryological series of man and monkeys at my disposal has led me to use these primates and especially man as the basis of my investigations. Therefore I will begin by trying to justify the above assertion by observations made upon the teeth of man and other Primates; after that I will give a number of examples to prove that this assertion holds good also with regard to other mammals. In fig. 26 ten successive sections are reproduced through the inferior lateral incisor of a human embryo of 39 mm. whole length. This embryo is registered in the collection as: Homo *Y*. The thickness of the sections is 10 μ. After the 10th section there followed three more through the same tooth showing a gradual diminishing of the enamel-organ. It was not necessary to reproduce these also.

In looking over the figures, it seems to me that the last of the series (fig. 26) is intelligible without further explanation, the enamel-organ possessing

the well-known form and being connected with superficial epithelial layers by means of the dental lamina.

Lateral from this the labio-gingival sheet (cf. the first essay for the meaning of this term) penetrates into the subjacent tissue.

The drawn sections show the form of the anterior half of the enamel-organ. In the first section (fig. 26 *b*) there is as yet no trace of the enamel-organ, only the dental lamina is cut through[1]. In the second section (fig. 26 *b*) there appears lateral to the dental lamina a heaping up of epithelial cells, which enlarging in the succeeding section (fig. 26 *c*) fuses in the fourth section (fig. 26 *d*) with the centre of the dental lamina, forming with this a crescentic epithelial formation at the end of the tooth-band.

This section is a very misleading one, for if some one had under observation only this section, he would be inclined to interpret it as a bell-shaped enamel-organ into the cavity of which the dental papilla was already deeply pushed. This interpretation, though a false one, becomes intelligible by the unquestionably existing agreement of the present section with that of a real bell-shaped enamel-organ. For the latter, when viewed in section, is also somewhat crescentic as that in fig. 26 *d*. And also in this stage of development of this enamel-organ the inner horn of the crescent seems to be formed by the terminal end of the tooth-band, while the outer bends outwards from it. Yet, the mistake in this interpretation of fig. 26 *d* is immediately shown by the next section. For here, from the end of the outer horn of the crescent, an offshoot emerges in a horizontal direction, approaching the end of the medial horn (fig. 26 *f*) and, finally, uniting with the same (fig. 26 *g*). By this process an enamel-organ is formed, ring-shaped in transverse section, the centre of which is filled up by mesenchymatous tissue. In the two next sections this centre gradually decreases (fig. 26 *h*, *i*) to disappear finally in the last section (fig. 26 *k*). The enamel-germ has now acquired the well-known form of a Florence flask. Immediately behind the section represented in fig. 26 *k*, the enamel-organ rapidly diminishes in size, as has already been mentioned.

This description of the structure of the enamel-organ in a very early stage of development differs somewhat from that usually found in odontological literature. Yet I wish to emphasise the fact that the structure described is not at all an exception or a special case, but is a phase of development which is passed through by every tooth in Primates as will be demonstrated later on. Only the details of it are not in all teeth so easy to observe as in the example chosen.

Recognition of this more complicated form of the enamel-organ is of fundamental value for the right understanding of the succeeding stages of development. And therefore we must try to get a clear and complete conception of it. This can be performed by building up in our mind the enamel-

[1] I wish to follow the custom in calling this epithelial formation the dental lamina. But as demonstrated in the first essay, its real signification is wider, because the gum at the oral surface of the alveolar ridge is produced by it.

organ represented in fig. 26 by superposition of the sections. On doing so, the enamel-organ presents itself as a low flask-like organ, with a broad base, slightly concave and with a niche-shaped dimple in its front side. In the present case the niche is still very shallow, only the three sections, *g*, *h*, *i* of fig. 26 running through it; but the whole organ is as yet a very minute one. This niche shall be distinguished henceforth as *enamel-niche.*

Now our first task is to demonstrate that the enamel-niche is a regularly occurring formation in an early stage of development of teeth in general, after which a description of its further destiny will follow and a discussion of its signification. To demonstrate the occurrence of the enamel-niche in the germ of the lower medial incisor, I give in fig. 27 six diagrams of sections through this tooth in a Macacus cynomolgus. Intentionally I choose this example, not only because it is in a somewhat further state of development than the preceding specimen, but also because, by using promiscuously preparations of man and monkeys the facts to be stated are demonstrated for the whole order of the Primates at once.

After the description of the diagrams in fig. 26, those in fig. 27 do not require detailed discussion. The question whether there is in this case also an enamel-niche is not a dubious one, it is clearly shown by diagrams *d* and *e*.

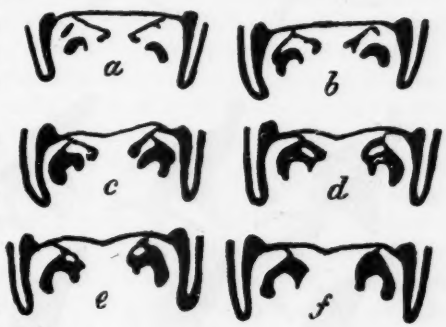


Fig. 27

This series of diagrams enables us to demonstrate the necessity of basing the study of the development of teeth always upon uninterrupted series of sections. In this case, for instance, the diagrams *b* and *c* might give rise to a quite incorrect interpretation. If any one had only these two sections at his disposal, he would take them for the germ of a milk tooth, and medial from this the dental lamina with the first trace of the germ of the successional tooth. That such an interpretation is a false one is at once demonstrated by the diagram *d*, though it must be admitted that the images are very misleading ones. The epithelial strand, interpreted as the dental lamina, is indeed the medial wall of the enamel-niche, not yet connected with the body of the enamel-organ.

Furthermore these diagrams illustrate unquestionably that the medial wall of the enamel-niche is in reality formed by the dental lamina itself. We will return to this question when we discuss the mode in which the enamel-niche is formed. For the present our purpose is only to demonstrate its occurrence.

Concerning the two next teeth I return to the genus Homo. In fig. 28 eight diagrams are represented from sections through the upper canine of the

human embryo, registered in my collection as: Homo *d. R.*, and in fig. 29 ten diagrams of sections through the germ of the lower canine from the human fetus registered in my collection as Homo *A*. I preferred to select for these teeth distinct embryos, because, by doing so, the proof is furnished that the occurrence of the enamel-niche is a general phenomenon, happening not occasionally in some fetuses. The embryo *A* to which the figure 29 relates was older than the embryo *d. R.* of fig. 28. The number of sections through the inferior canine of the former was therefore larger than that through the superior canine of fig. 28. Therefore in fig. 29 all the sections

Fig. 28

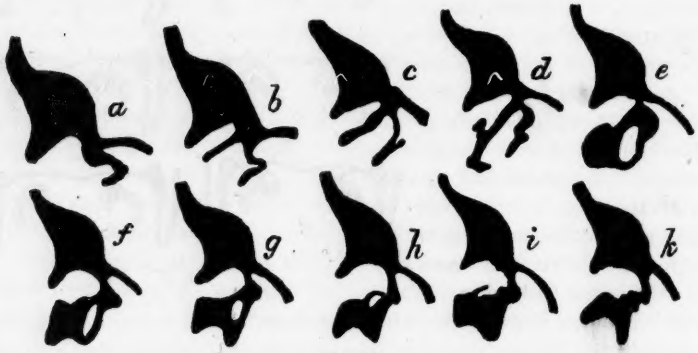


Fig. 29

through the frontal part of the tooth-germ are not reproduced. I choose such as are necessary to give a sufficient idea of the manner in which the enamel-niche is formed in this tooth and—as must be emphasised—in the present stage of development. For, as will be demonstrated, in this stage of development the enamel-niche has already passed from its first stage into that in which it is commonly found, being transformed from a niche into a tunnel.

That the enamel-niche occurs also in the upper canine is undoubtedly settled by fig. 28. The thickness of the sections being 15 μ, it becomes evident that the niche in this case was but a very shallow dimple. This circumstance is a very lucky one, for it gives us an insight into the very first stage of the

niche, and we shall make use of this case in our discussion of the mode of formation of the niche.

A somewhat different state of the niche is shown by the diagrams in fig. 29, relating to the inferior canine of man. The sections also had a thickness of 15 μ, and between the first and last diagram there were in reality still ten sections which are not represented. When the diagrams of fig. 29 are examined and compared with the description of the enamel-organ in its succeeding stages of development as commonly met with in literature, it is not easy to understand their meaning. The diagram *a* showing only the dental lamina connected with the surface epithelium is intelligible without any explanation. On the contrary the diagram *b* offers a difficulty. For, lateral from the dental lamina a second strand of cells has grown into the mesenchyme, going out from the surface epithelium, close to the spot where the base of the dental lamina is attached to the superficial epithelium. And this latter, lateral strand, elongates until it becomes even larger than the true dental lamina, as shown by the diagrams *c* and *d*. If one had only these two sections at his disposal, surely it would be quite impossible to understand them. In diagram *e* two changes have occurred: from the lateral band a horizontal process—already seen in the diagram *d*—has sprung, and by the union of this with the free edge of the dental lamina, the enamel-niche is formed. There is besides a considerable thickening at the outer side of the lateral strand. It is clear that in this stage of development the outer wall of the enamel-niche is formed by the lateral strand of cells, whilst the inner wall is formed by the dental lamina, a fact already known to us. Now it is very interesting to notice the position of the niche in the sections behind, as shown by the diagrams *f*, *g* and *h*. The niche is narrowed gradually, but at the same time it moves upwards and laterally, till finally its outer wall is formed by a thin layer of epithelial cells, as seen in diagram *h*. In the next diagram this wall is burst and the niche has opened on the outer side of the enamel-organ. In this stage of development there is in reality no longer question of an enamel-*niche*, for its backwall is perforated and it is transformed into a short tunnel running through the anterior half of the enamel-organ in a slightly oblique direction. This fact is of fundamental significance. For in consequence of the perforation of the backwall of the niche, the enamel organ has got a double junction with the dental lamina; a medial and a lateral one. The medial is formed by the dental lamina itself, and the lateral by a thin band of epithelial cells originally participating in the building up of the enamel-organ. It is necessary to distinguish the bands, connecting the enamel-organ with the dental lamina, by distinct names. The lateral band I will denominate *the outer enamel-band* and the medial *the inner enamel-band.* In the sequel of this essay these bands will be amply discussed. But I must first return to the enamel-niche in its original state.

We have stated its occurrence in the lower incisors and in the canines. As to the superior incisors it is somewhat more troublesome to demonstrate their presence in an early stage of development of man and monkeys. For, the niche

being a dimple in the medial side of the enamel-organ, transverse sections are not the most suitable to demonstrate its presence in these teeth, owing to the fact that they are transversely implanted in the premaxillary bone, and the germs already occupy this position. In older stages, when the niche is transformed into a tunnel, and the whole germ of the tooth is enlarged, this difficulty is removed. As a more suitable demonstrating object I choose the enamel-organ of the superior incisors of a Prosimian, in which these teeth are implanted in a more sagittal plane. In fig. 30 nine diagrams are represented of sections through the second superior incisor of a Propithecus (series *B* of my

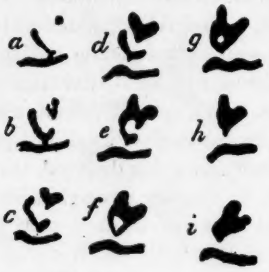


Fig. 30

Fig. 31

collection) and in fig. 31 six diagrams of sections through the third incisor of a Lemur melanocephalus (series *A* of my collection). By these figures it is proved that the enamel-organs of these teeth also are provided with an enamel-niche. But that it is, under favourable circumstances, not at all impossible to observe the niche in the upper incisors of man is proved by fig. 32, showing six diagrams of sections through the enamel-organ of the lateral upper incisor of a human fetus (series *B* of my collection, thickness of the sections: 25 μ). The plane of section in this case was slightly oblique.

Fig. 32

From the foregoing it may safely be concluded that the enamel-niche is met with in the germ of all the monocuspidate teeth of the milk-dentition of Primates. It would be very easy for me to supply more examples, but the foregoing are, I believe, sufficient to prove the niche to be a normal phenomenon in the development of the teeth. Besides, any one possessing suitable material and uninterrupted series may produce further proofs himself. The establishment of the niche in its primitive state in the enamel-organs of molars is not so easy a matter as in the monocuspidates. For as a rule the germs of the molars are situated close to the surface epithelium, the dental lamina being shorter; it even happens not seldom that in the region of the germ of a

molar the dental bond seems to be absent totally, the germ taking origin directly from the surface epithelium. This fact renders the interpretation of the appearances often somewhat troublesome. Moreover, the niche itself in the enamel-organ of molars behaves so as to render its demonstration rather difficult. Firstly it seems to exist in these tooth-germs only a very short time, passing rapidly into its second state, namely the canal or tunnel already alluded to.

And secondly, it seems that in the germs of molars, the niche is not always situated in the mesial or frontal side of the germ, but occasionally the dimple appears at the posterior side of the germ. This variability in the situation of the niche is a very indifferent fact, for whether beginning at the front side or at the back side of the organ it is in all cases soon transformed into a canal by perforating the organ either in a forward or in a backward direction.

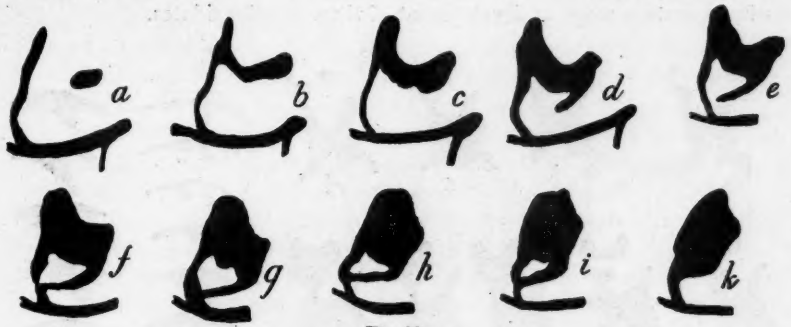


Fig. 33

The above facts are illustrated by figs. 33 and 34. In fig. 33 ten sections are represented through the enamel-organ of the second superior milk molar of an embryo of Mycetes (Mycetes *A* of my collection) and in fig. 34 eight sections through the enamel organ of the third superior milk molar of the same object. Now in both figures the presence of the enamel-niche is obvious. But on comparing the figures it becomes clear that in the second milk molar (fig. 33) the entrance to the niche is situated at the front side of the organ. The sections figured are taken from the anterior half of the germ. And in this part of the germ the niche diminishes in size, as it is traced backward until it finally disappears. The germ of the third milk molar on the contrary (fig. 37) shows no trace of a niche in its anterior half, till behind the middle of the germ the niche appears as a small opening in the centre of the organ which increases in size and has its entrance at the back side of the organ. In the beginning of my investigation when my attention had only recently been drawn to this formation, the variable situation of the niche in the enamel-

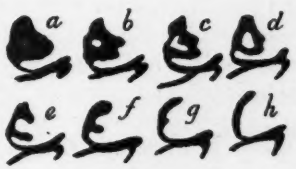


Fig. 34

organs of molar teeth rendered the phenomena not always easy to understand, the object being not always in the most suitable state of development to procure a clear insight into the relations. But in examining a larger number of series this point became more intelligible to me. I thought it necessary to intercalate this remark as a warning to the reader anxious to check the correctness of my description, that he must procure himself a rather numerous series of specimens of different ages. Only in this manner will he be able to observe all the particular facts described above.

As a last example of an enamel-niche in its first and simple state in a molar, I give in fig. 35 nine sections through the anterior half of the first superior molar of a human embryo (series *A* of my collection).

After the preceding descriptions these diagrams do not require a particular elucidation. They prove that in human molars also the niche is present during a certain stage of development of these multicupidates.

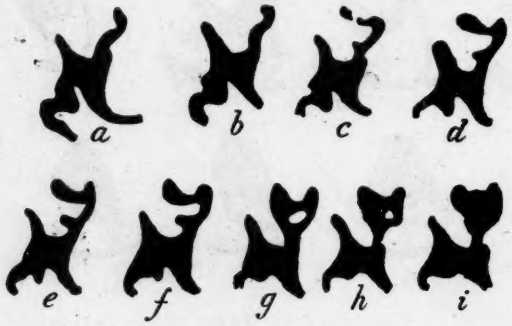


Fig. 35

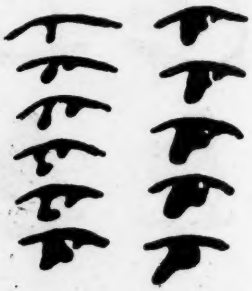


Fig. 36

I have already made allusion to the fact that in some Primates a true dental lamina is absent, the germs of the teeth originating immediately from the deep layer of the surface epithelium. Such a Primate is, for instance, the Semnopithecus. Now it is a fact worthy of note, that in such cases also the enamel-niche makes its appearance. For by such cases it is proved that the niche is not a formation of the dental lamina, but that it belongs exclusively to the enamel-organ, being characteristic of an early stage of its development. In case of absence of the dental lamina the niche is of a somewhat irregular form and its mode of formation is also not a typical one. Fig. 36 gives a sufficient illustration of such a case.

The diagrams show a number of sections through the enamel-organ of the first inferior molar tooth of a Semnopithecus maurus in an early stage of development.

By the foregoing facts I believe to have succeeded in my attempt to prove that the development of the enamel-organ of teeth in Primates is not so simple a fact as may be concluded from the descriptions given in the textbooks of

Anatomy. In none of these have I met with any allusion to the formation of the enamel-niche. In German literature it was recognised at nearly the same time by myself[1] and by Ahrens[2].

This author, however, had restricted his investigation to human teeth only, whereas I have examined a large number of other mammals and have demonstrated that the niche is a common appearance in the organ of nearly all the objects studied by me.

The examples given all agree in one point, namely, that they relate to milk teeth of the Primates. And the question arises, whether this appearance is restricted to this set of teeth only, or if in the enamel-organ of the successional teeth a niche is formed. The answer to this question must be in the affirmative but the demonstration of the correctness of this assertion is not easy. For it is a rather troublesome matter to obtain an uninterrupted series of sections through the germs of these teeth, and having succeeded in it, it is a mere chance that the object was in the proper stage of development.

Yet, I have been able to gather some examples out of my collection of preparations of which I now will give a brief account.

In figs. 37, 38 and 39 three examples of the niches in the enamel-organ of permanent teeth are represented. Fig. 37 relates to the lower permanent canine of a Galeopithecus (series *B* of my collection). Fig. 37*a* gives a general view of the situation of the enamel-organ of this tooth. The surface epithelium is already differentiated and the germ of this tooth lies free in the mesenchyme of the jaw. Lateral to it the fang of the milk canine is cut as a cap of dentine, containing pulp-mass. The germ of the permanent canine is of a conical form with a ring-shaped top. To get a more detailed idea of this niche in fig. 37*b*, *c*, *d* and *e*, four sections through this enamel-organ are drawn on a magnified scale. And from these figures it becomes obvious that the niche was no longer in its primitive state of development, fig. 37 *e*, showing the perforation of the lateral wall of the niche. Instead of a niche, we have here already to do with the enamel-canal. This detail, however, is of no importance. In general the study of my series has convinced me that in the germs of the successional teeth the enamel-niche in its simple state is small and of short duration, being soon transformed into a canal.

This is illustrated by the four outlines of fig. 38, showing sections through the enamel-germ of the superior medial permanent incisor of man (series 2 of my collection). I have represented the germs of both sides *in situ*, and included in the figures also the enamel-organs of the milk incisor, situated lateral to those of the successional teeth. It is obvious that in the permanent incisors the enamel-niche appears in a very early stage of development, the whole organ being still very minute. This circumstance renders the establishment of the

[1] L. Bolk, *Odontologische Studien I, Die Ontogenre der Primatenzähne.* Zena. Gustav Fischer. 1913.

[2] H. Ahrens. "Die Entwicklung der menschlichen Zähne," *Anat. Hefte*, Band 48. Wiesbaden. 1913.

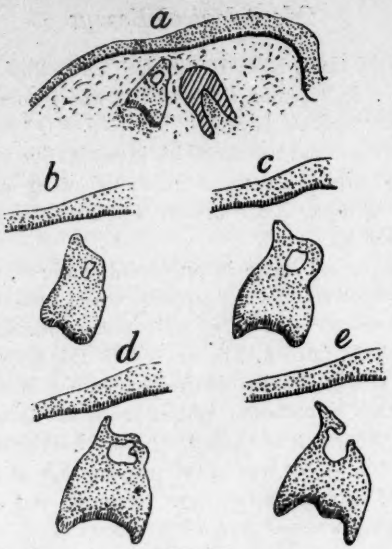


Fig. 37

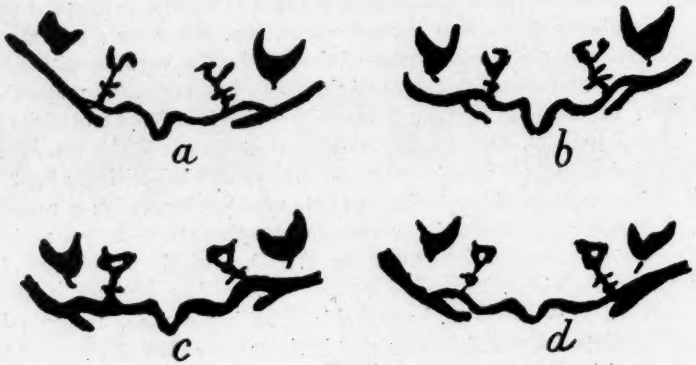


Fig. 38

Fig. 39

presence of the niche in such organs rather difficult. A very fine specimen of an enamel-niche in the germ of a permanent tooth is finally represented in fig. 39, showing a number of diagrams of succeeding sections through the enamel-organ of the inferior first permanent molar of Mycetes (series *B* of my collection). The diagrams are arranged in vertical rows. In this case we have to do with a niche whose backwall is already perforated, as shown by the two diagrams of the last row.

With regard to theoretical considerations upon the morphological signification of the enamel-niche, the statement of its occurrence in the organ of permanent teeth is of the utmost interest. And therefore I will here add that Sicher has lately demonstrated the presence of an enamel-niche in the permanent teeth of the mole[1].

From the foregoing it may safely be concluded that the development of the enamel-organ in Primates (and as will be demonstrated later on also in other mammals) does not happen in such a simple manner as would be concluded from the descriptions given in the textbooks of Embryology. It is of a more complicated nature, and owing to the appearance of the enamel-niche, the relation between the enamel-organ and the dental lamina becomes somewhat more intricate than would be concluded from the current descriptions. Our first task will now be to demonstrate this by dealing with the principal points in the further behaviour of the enamel-niche.

There was already occasion in the foregoing discussion to remark that the enamel-niche as such is but of short duration. For, by penetrating gradually deeper into the enamel-organ, its backwall becomes successively thinner, until at last it is perforated and instead of a niche the enamel-organ is provided with a canal of conical form.

An organ in which the perforation has just been completed is but rarely seen. Yet, amongst my series of human embryos, I have found some examples of this process, two of which are represented in figs. 40 and 41. The diagrams in fig. 40 relate to the first upper milk molar of man (series *C* of my collection) and those in fig. 41 to the lower canine of man (series *V*). In both figures the diagrams are arranged in horizontal rows, and in both the last diagram but one is that of the section just passing through the very point where the niche perforates its backwall. The opening is still a very narrow one.

But even if such stages were not found, the transformation of the niche into a canal cannot be at all dubious, for, in all stages of development that have proceeded somewhat further than these, of which a description has been given, it is a very easy matter to observe the canal-shaped formation alluded to passing through the enamel-organ. Only, to get a complete idea of this formation, it is necessary to have at our disposal a considerable collection of preparations, for the enamel-canal also undergoes great changes in the course of its own development, and owing to the enlargement of the enamel-organs.

To depict the history of the enamel-canal in a brief and simple manner, it

[1] Harry Sicher, "Die Entwicklung des Gebisses von Talpa europaea," *Anat. Hefte*, Band 54.

seems sufficient to me to base my explanation upon a series of figures, showing different stages of development of enamel-organs.

It is superfluous to figure all sections through an organ of these older stages. I will confine myself to representing the figures necessary to understand the course of development.

In its earliest state the enamel-niche appears as a dimple situated in the

Fig. 40

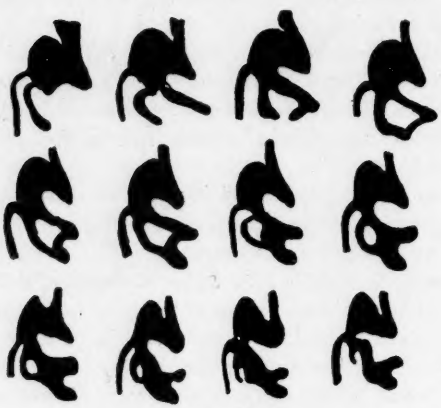


Fig. 41

top half of the enamel-organ—at this time still conical. And during the time immediately after the perforation of its backwall this is still nearly the case.

In the course of the further development the first change concerning the enamel-canal is its often considerable widening, connected in most cases with a change in its position. In the earlier stages the niche or the canal is situated not infrequently rather symmetrically in the enamel-organ. But in older stages it has a more asymmetrical position and is situated as a rule in the lingual half of the enamel-organ. This is clearly shown by the figs. 42, 43, 46 and 47. This

situation is due to the fact that the proper enamel-organ is developing and enlarging principally in a buccal direction.

That this mode of development does however not always take place is shewn by the figs. 44, 45, 48 and 49, to which I will return later on. By the dilatation of the enamel-canal the character of the whole germ is very much changed. For the canal is now enclosed between a very thin lingual wall, which is indeed the prolongation of the dental lamina, and the enamel-organ itself.

This condition is very clearly demonstrated by fig. 42, representing a section through the medial upper incisor of Mycetes (Mycetes *A* of my collection) and by fig. 43 representing a section through the same tooth of an older embryo of this genus (Mycetes *B*). If one takes into consideration that in both cases there exists a real canal running through the enamel-germ, and that the thin lingual wall of this canal is the prolongation of the dental lamina, it is obvious that one may describe this state as an enamel-organ having not a single, but two connections with that lamina, a lateral and a medial one. That the lingual wall of the canal is really a part of the dental lamina is demonstrated by figs. 46 and 47, the former being a transverse section of a milk molar of Mycetes *A*, and the latter a sagittal section through the germ of the upper medial incisor of a human embryo (series *M*). For at the point at which the dental lamina is connected with the lingual side of the enamel-organ, an epithelial outgrowth may be seen, and without doubt this outgrowth is the commencement of the germ of the successional tooth. Now for the sake of intelligibility and to facilitate further description it is necessary to introduce some morphological expressions. In describing the tooth-germs in figs. 46 and 47, one may distinguish the enamel-organ proper and a system of epithelial strands.

The existence of these epithelial strands is partly due to the formation of the enamel-niche as a predecessor of the enamel-canal. Now the niche, as well as the canal, are differentiations formed in the primitive enamel-organ; in an earlier stage the walls of the canal took part in the building up of the enamel-organ. And so in the history of the development of the enamel-organ two phases must be distinguished: the primitive state in which there is not yet an enamel-niche and *a fortiori* no enamel-canal and a secondary state in which it is obvious that the enamel-organ represented in figs. 46 and 47 is not identical with the organ in its earliest state. For, in the latter the walls of the enamel-canal are differentiated. This fact requires us to distinguish a primitive from a secondary enamel-organ. The primitive is the club-shaped thickening of the tooth-band before the dimple of the enamel-niche has made its impression into it. By the formation of the enamel-canal this primitive organ is differentiated into the secondary enamel-organ and a system of strands. These strands—a fact not to be forgotten—are built up from elements, which originally belonged to the primitive organ.

This point settled, we will proceed to consider the system of strands. The diagrams represented in figs. 46 and 47 show relations very typical of a certain

stage of development of the teeth, and easily to be found in embryos of appropriate ages. First there is an epithelial strand, emerging from the surface epithelium and bifurcating into two strands, which unite with the secondary enamel-organ. So the strand-system is composed of three elements which may be demonstrated by distinct names. The strand which emerges from the surface epithelium to its point of bifurcation is the true dental lamina, which I will further distinguish as *common dental band.* The two other strands are special formations, belonging, as having taken their origin from the primitive enamel-organ, to a distinct enamel-germ. I shall distinguish these two strands as the "lateral" and the "medial" enamel strand. The latter is the prolongation of the common dental band, at least in younger stages of development.

Fig. 42

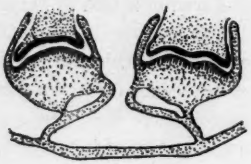


Fig. 43

Fig. 44

Fig. 45

Fig. 46

Fig. 47

Fig. 48

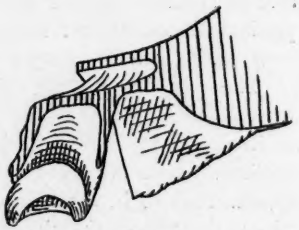


Fig. 49

The proposed nomenclature, which facilitates the further description in no mean degree, is, I believe, a rational one, making due allowance for the morphological value and genetical signification of each of the elements. Returning to our proper subject, the sections seen in figs. 44 and 45 require a closer consideration. Both figures represent sections through the enamel-organ of the first upper molar tooth of man, the specimen in fig. 45 being somewhat further developed, as derived from an older embryo (fig. 44, series *T*, and fig. 45, series *G* of my collection). To understand these figures, I remind the reader of the fact, already mentioned, that the primitive dental lamina of molar teeth is frequently very short, the primitive enamel-organ of these teeth being therefore attracted immediately to the surface epithelium.

Taking this fact into consideration the conditions in figs. 44 and 45 are easily understood. The common dental band being absent, the top of the primitive enamel-organ reached to the surface epithelium. And, as amply demonstrated, the enamel-niche begins as a dimple in the top part of the organ. Thus this niche, and also the enamel-canal, is situated immediately beneath the surface epithelium. Such a case is represented by fig. 44. And because during the further development the canal is enlarging itself, it becomes partly limited by the surface epithelium as shown in fig. 45. In such cases the secondary enamel-organ is attached to this epithelial layer by the two distinct strands, without the agency of a common dental band.

The conditions just described do not occur only in molar teeth, but now and then also in front-teeth as, for instance, the American monkey, Chrysothrix, may prove. Fig. 48 gives a section through the germ of $\bar{i}$, of this animal[1]. The enamel-canal in this case is very large, and were one ignorant of the development process of the organ, as described in the foregoing pages, it would be very difficult to understand this figure. I suppose I have now proved in a sufficient manner the fact that the evolution of the enamel-organ in Primates is not so simple a matter as usually described in literature.

As the principal fact, added to our present knowledge, I consider the circumstance that in this evolution two phases must be distinguished: that of the primitive and that of the secondary enamel-organ, the former being differentiated into the latter and a system of bands.

To get a more complete idea of the shape of the secondary enamel-organ with its epithelial bands, I have constructed in the well-known manner some wax models, two of which are represented in the figs. 49 and 50. The figure 49 shows the wax reconstruction of the enamel-organ of $\bar{i}$, of a human embryo. In this rather young stage there is not yet an enamel-canal; above the secondary enamel-organ one looks into the hollow of the enamel-niche. A stage of further development is represented by figs. 50*a* and 50*b*, being the reconstruction of the $\bar{M}_3$ of a Chrysothrix. In this case there is a well formed enamel-canal with a complete system of bands, the common dental band emerging from the layer of surface epithelium and dividing into the internal and external enamel strand. In fig. 50 *a* the reconstruction is seen from the front side, in fig. 50*b* from the buccal side. By the latter figure it is clearly shown that the external enamel strand is a special one, it is confined to the enamel-organ, whereas the internal strand is a real part of the common tooth-band.

The further history of the system of bands can be shortly exposed with the aid of figs. 52*a* and 52*b*. While the secondary enamel-organ is gradually enlarging, and the well-known histogenetical transformations take place into

[1] I wish to give here a short explanation of the manner in which the elements of dentition will be indicated in this and all following essays. The teeth of the milk-dentition are indicated by the minuscules $\underline{i}$, $\underline{c}$, $\underline{m}$; the permanent teeth by the *majuscules* $\underline{I}$, $\underline{C}$, $\underline{P}$, $\underline{M}$. A tooth of the lower jaw is recognisable by a dash above the symbol, those of the upper jaw by a dash beneath it. Thus, for instance, the second milk incisor of the lower jaw is written as $\bar{i}_2$, the third permanent molar of the upper jaw is $\underline{M}_3$.

it, the enamel-canal becomes more and more spacious. And in those cases in which the lateral enamel strand was attached near to the base of the organ, the top of the enlarging organ vaults into the widening canal. By this filling up of the canal, its outer wall—that is the lateral enamel strand—approaching gradually the lateral side of the organ, finally covers the same, as clearly shown by fig. 52 *b* representing a section through the $\underline{m}_3$ of a Canis familiaris (series *A*). Now, in the meanwhile this outer wall has been the seat of considerable changes. These changes were of a degenerative nature. Instead of being a flat and complete sheet, it becomes cribriform. The surrounding mesenchymatous

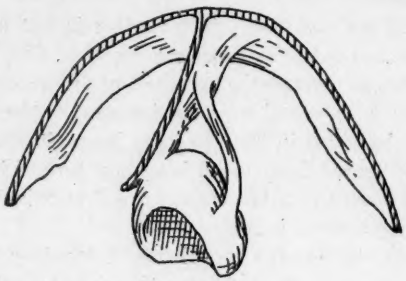


Fig. 50 *a*

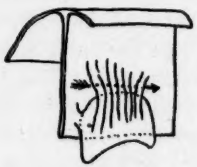


Fig. 50 *b*

Fig. 52 *a*

Fig. 51

Fig. 52 *b*

tissue penetrates it in an abundant manner, so that at last the lateral enamel strand is broken up into a large number of fragments or epithelial islets. In this condition it acquires contact with the outer side of the enamel-organ, the fragments are situated immediately against its external epithelium and appear as a layer of irregular excrescences, projecting from the buccal side of the organ. Now and then, however, a more primitive condition persists, the lateral enamel strand remaining independent of the outer side of the organ, and extending as a layer of epithelial islets at some distance from it, reaching from

the base of the organ to the common dental band. This condition is shown by fig. 52*a* ($\overline{m}$, of a Mycetes) and fig. 58 ($\bar{\imath}$ of Equus caballus, series *D*).

In the course of the further development, the common dental band and its prolongation, the medial enamel strand, degenerate and atrophy. The manner in which this process goes on is similar to that in the lateral enamel strand. In the meantime the organ recedes from the medial enamel strand; during a short time it is still connected with it by a narrow line of cells, by the interruption of which the organ becomes quite independent of the system of bands. To our knowledge of this well-known process, I have nothing to add.

As pointed out before, we intended, after the description of the earlier stages of tooth-genesis in Primates in a more detailed manner, to prove that the ontogenetical conditions, which we have met with in this group of mammals, occur also in the other groups. As we can do so in a brief account, there is no need of the pointing out afresh of all observations which I have made concerning these points, and I will confine myself to giving some examples from different groups, which I choose among my considerable collection of series of mammalian embryos. In doing so I accomplish, as I believe, my purpose: to demonstrate that the enamel-niche and canal are universal phenomena in the tooth-genesis of mammals. The conviction, however, that the enamel-organ, during a short period of tooth-genesis, has a double connection with the tooth-band, can only be acquired by examining a large number of mammalian embryos of different species and different ages. For it may be repeated that the recognition of the presence either of the niche or of the canal is not always very easy, the development of both being often rudimentary. Of the general occurrence of niche and canal I was so strongly convinced, that it was a very interesting and surprising fact to me, to find that there are forms in which any trace of a niche or canal is wanting. I will advance two examples of these exceptions. The first concerns the milk teeth of Cheiroptera. Of this group I have studied a number of series, in close stages of development, of the Malayan form: Roussettus amplexicaudatus. And it is very interesting, that while I looked in vain for an enamel-niche or canal in the organs of the set of milk teeth, the organs of the successional teeth behave quite regularly, as may be seen in fig. 56, showing a section through the anlage of P_2 (series *C* of my collection) in which the double connection between tooth-band and enamel-organ is obvious. There is a short enamel-canal running in the typical manner through the top part of the organ.

This case is a very welcome one from another point of view, for it is a further proof of the occurrence of the enamel-canal in the organs of permanent teeth.

I believe I know the reason of this lack of an enamel-niche in the milk teeth of Cheiroptera, but I think it is premature to advance my opinion upon this point, before I have given a plain and integral exposition of my views upon the genetical signification of the enamel-canal in general. And so I will return to the facts later on.

The second exception concerns the dentition of Marsupials. Here also the attempt to find an enamel-niche or canal is sometimes in vain. As in many other features so in this point the Marsupialia behave in a very peculiar manner. For while in one tooth the smallest vestige of a canal or a niche is absent, the succeeding tooth may show either in a most excellent manner. This is demonstrated, for instance, by fig. 54, in which three sections are drawn of I_3 of Perameles nasuta. I will not insist upon these phenomena in this place, because the dentition of Marsupialia will be, in the following essays, more than once an object of special inquiry, and on one of these occasions the above-mentioned peculiarity will be taken into detailed consideration.

Now we will proceed to give some examples of an enamel-niche or canal in other mammals. The first "anlage" of the niche in the enamel-organ of the cow is sketched in fig. 53. The diagrams represent eight successive sections through the organ of m_1. As clearly shown, this molar has taken origin in the ordinary way immediately from the surface-epithelium, whereby the niche—being still rather shallow—is bounded partially by this layer. The figs. 51 and 58 are drawn after preparations of embryos of the horse. Fig. 51 shows the entrance to the niche in the enamel-organ of $\bar{i}$ and fig. 58 a section through the enamel-canal of an $\bar{i}$, of an older fetus. The lateral dental strand of the horse attaches itself to the secondary organ very near to its base, that is to say the enamel-niche does not develop as usually in the apex of the primary organ, but is situated in its buccal part.

This is to be seen in the diagrams of fig. 51. And during the further development—in which the canal is much enlarged and partially filled up by the secondary organ—the lateral enamel strand does not lay itself against the outer side of the secondary organ, but there always remains a cleft-shaped space between the organ and the strand. This condition, clearly shown by fig. 58, was met with—as already referred to—also in some monkeys. A somewhat different condition, corresponding more to the normal state in monkeys, is offered by the dog. In this animal the niche develops, as is the rule in Primates, in the apex of the primary enamel-organ, and the two special strands therefore attach to the secondary organ in a more symmetrical manner as shown by figs. 55 *a* and 55 *b*. Similar conditions are offered by the teeth-germs of Hyrax. In fig. 55 *c* a section is represented through the germ of i_2 of this animal. Also in Ovis the canal is present as is demonstrated by the section through $\bar{m}_2$, drawn in fig. 57.

In the foregoing, I think, sufficient proofs are furnished, to establish the truth of my assertion that the development of an enamel-niche and the transformation of it into a canal is a process proper to all mammals save some exceptions. And on account of the universality of these phenomena it can hardly be doubted that they are of prime significance in the phylogenetical history of mammalian teeth. This supposition is strengthened by the fact that during the development of the teeth of lower vertebrates, including reptiles,

Fig. 53

Fig. 54

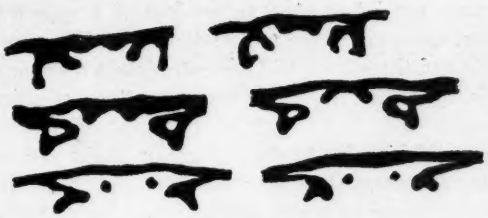


Fig. 55 *a*

Fig. 55 *c*

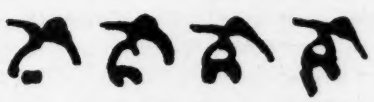


Fig. 55 *b*

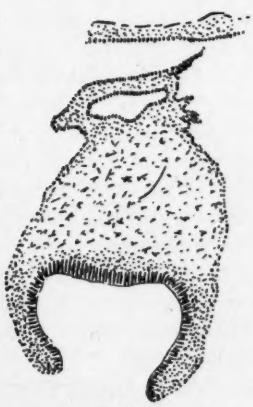


Fig. 56

Fig. 57

Fig. 58

not the least trace of a niche or canal is to be seen. It is a phenomenon restricted to the tooth-genesis of mammals and therefore in some way or other it must be a consequence of the manner in which the evolution from reptilian to mammalian tooth happened.

After the systematical description of the enamel-niche and canal, and the special epithelial strands bounding the latter, at present only a few lines can be devoted to the question whether these formations are really entirely unknown in literature. The answer to this question can be very short. The development of the enamel-niche and its transformation into a canal as a typical phenomenon in the tooth-genesis of mammals was quite unknown; it is a new fact added to our knowledge.

But the rudimentary fragments of the lateral enamel strand have already been observed by many investigators (Woodward, Kükenthal, Adloff). And by these authors the fragments are interpreted as vestiges of a supposed hypothetical pre-milk-dentition which will be the subject of a thorough enquiry in one of the succeeding essays and therefore I will not enter into a discussion of the value of this hypothesis, restricting myself for the present to a mention of this view.

The second phenomenon to which I wish to draw attention in the present essay is very different from the foregoing. It concerns the histogenetical differentiation of the enamel-organ. This process may be supposed to be generally well-known. Soon after the investment of the top of the dental papilla by the enamel-organ, the rounded undifferentiated cells, which build up the latter, begin to arrange themselves. Immediately upon the papilla is formed the layer of cylindrical ameloblasts, the superficial more flattened cells arrange themselves as the layer of external epithelium covering the mass of still undifferentiated cells, from which the layer of intermediate cells and finally the stellate reticulum or pulp-mass will take its origin.

Now it is to the last mentioned process—the formation of the stellate reticulum—that I wish to draw special attention, because the mode of origin of this mass, as observed by me, does not agree with the current opinion about it. This opinion is expressed very well in p. 140 of the 7th edition of Tomes' *Manual of Dental Anatomy*, where we read as follows: "The cells on the periphery of the enamel organ remain prismatic, but those in the centre become transformed into a stellate network. This conversion of the cells into a stellate reticulum is most marked quite in the centre of the enamel organ. The transformation of the cells occupying the centre and constituting the bulk of the enamel organ into a stellate reticulum goes on progressing from the centre outwards, but it stops short of reaching the layer of columnar cells which constitute the surface of the enamel organ, next to the dentine papilla. A narrow layer of unaltered cells remains between the stellate cells and the columnar enamel cells and is known as the 'stratum intermedium.'"

From this quotation I wish to emphasise the fact that according to this description there should be in the enamel-organ but a single point where the

transformation into a stellate reticulum begins, and from which the process would progress. This point is situated in the centre of the organ.

My observations disagree with this opinion. I have found that as a rule there is not a single centre, but that there are two centres in the enamel-organ from which the transformation into the tissue of stellate cells radiates. According to their situation these centres may be distinguished as a lingual and a buccal one. In dealing with and representing a number of my observations concerning this phenomenon I hope to furnish sufficient proofs of this assertion.

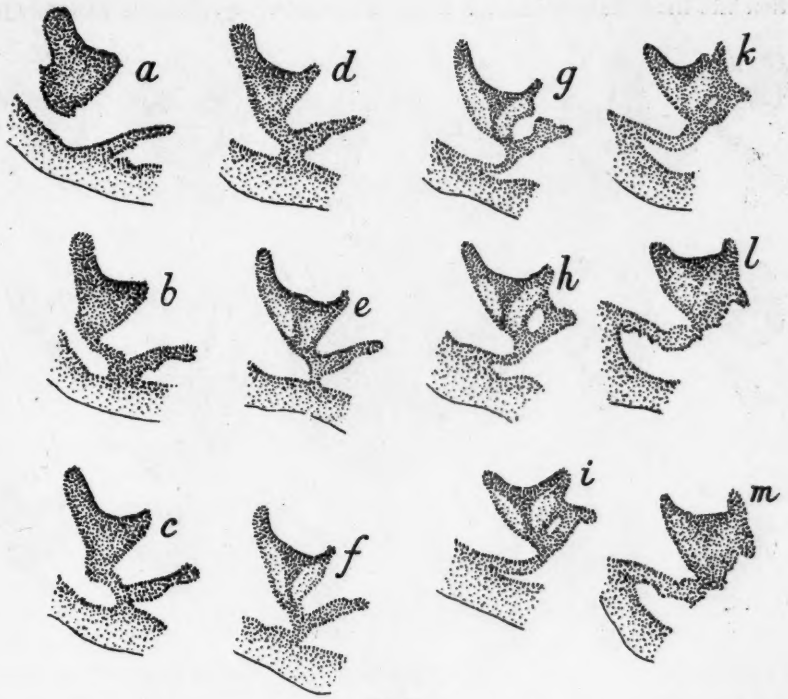


Fig. 59

I begin by communicating some observations made upon human embryos, because it was on this material that I made my first observations, and further, because human embryological material certainly is at hand in every anatomical or embryological institute, rendering my assertions easily controlable.

The starting point of the discussion may be furnished by the three series of sections through the tooth-germs of man in figs. 59, 60 and 61. Fig. 59 concerns the enamel-organ of an $\underline{i}$, fig. 60 that of a $\overline{m}_1$, and fig. 61 that of a $\underline{c}$. Each of these figures shows also the presence of the enamel-niche, to

which point however I do not wish to return. In looking over the first series of diagrams drawn in fig. 59, it is clear that the histological differentiation of the enamel-organ is still in its beginning. There is a well differentiated layer of columnar cells or ameloblasts, but for the rest the cells of the organ and of the dental lamina still possess their primitive rounded form. The first three sections of fig. 59 do not offer any particularity, but in the fourth section of the series (fig. 59 *d*) there appears in the centre of the organ a clearing up of the tissue, the heaping up of the nuclei becoming here somewhat less dense. Without doubt this is to be considered as the very beginning of the transformation into the stellate reticulum. In the next section (fig. 59 *e*) this clearing up

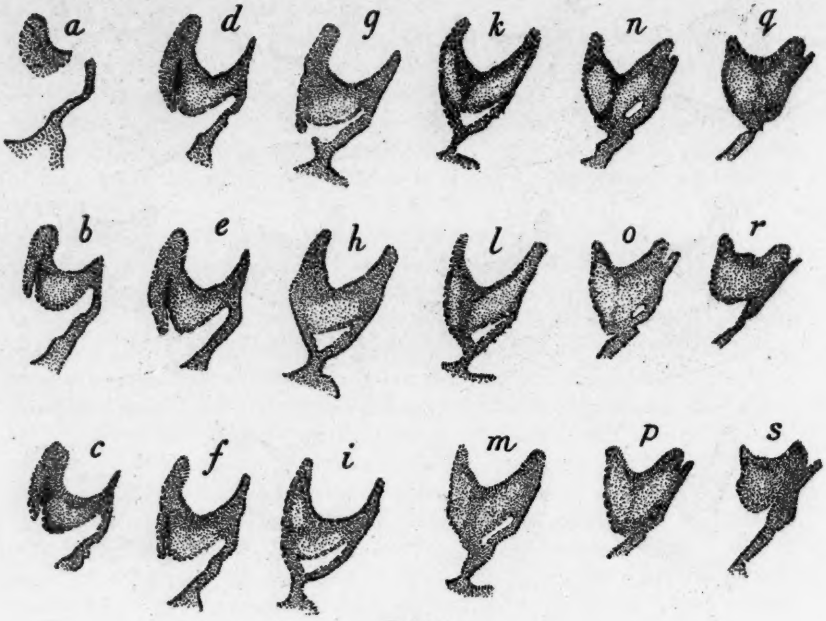


Fig. 60

is more pronounced but now it becomes obvious that the cellular elements, lying in the axes of the organ, do not participate in this process, so that there remains a layer of densely packed nuclei extending from the apex of the organ to the middle of its base. By this layer the centre of clearing is divided into two parts, a lingual and a buccal one.

Examining the succeeding sections it is evident that this compact layer of cells extends through the enamel-organ in a sagittal direction, disappearing in its posterior part, in which the organ is constituted anew by a very dense mass of cells.

I think the drawings in fig. 59 prove in a very clear manner this pulp-

formation as not beginning at a single central point of the organ, but from two centres, whereas it is exactly the central or axial elements of the organ that do not participate in this process, remaining on the contrary a more dense formation.

This compact layer of cells constitutes a separating wall or septum between the two centres of pulp-formation and accordingly in the sequel will be denominated as *enamel-septum*.

Now before beginning the inquiry about the further development and peculiarities of this septum, I wish to demonstrate its presence in man and in some other mammals by some other examples.

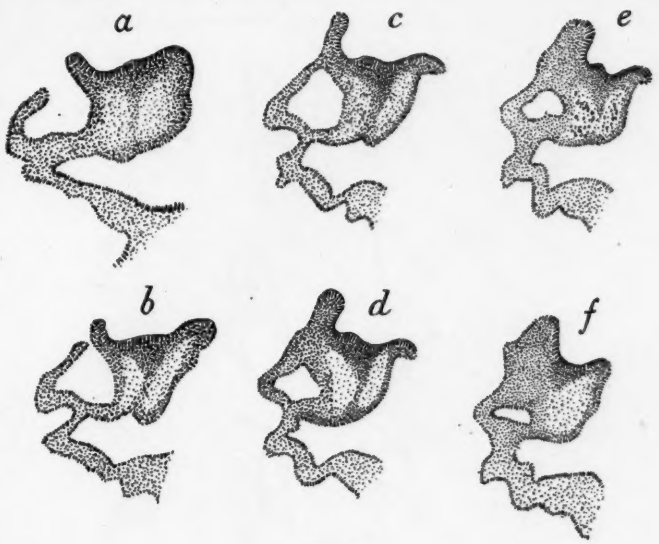


Fig. 61

In fig. 60 eighteen succeeding sections through the germ of $\overline{m}_1$ of a human embryo are sketched. And these sketches too show that there are two centres in which the pulp-formation begins. In the sketches 60 *c* to 60 *h* there is but one centre to be seen, situated somewhat excentrically in the lingual part of the organ. In fig. 60 *e* a second centre appears in the buccal half of the organ quite independent of the former. From fig. 60 *k* to fig. 60 *q* both centres are separated from each other by the enamel-septum. In the last mentioned figure the lingual centre disappears and only the hindmost part of the buccal is to be seen in the two last sketches. It is obvious that in this case the septum had a somewhat oblique direction, with the result that in the anterior part only the lingual and in the posterior part of the organ only the buccal centre was cut through.

The fact that in this case also there is still an enamel-niche and not yet an enamel-canal, proves that the organ is still in a very early stage of its development. I lay stress upon this fact for—as will soon be demonstrated—the septum is not a persistent formation of the enamel-organ, it is of a transitory nature. Therefore to observe it, one must select the material with care.

As a third example of the double pulp-centre in the enamel-organ of man, six sections through the organ of *c* are sketched in fig. 61. This specimen was selected in order to draw attention to a peculiarity of the external form of the organ, often observed in connection with the septum.

In figs. 61*b* and 61*e* a dimple is visible in the apex of the organ corresponding with the attachment of the septum. The surface of the organ seems

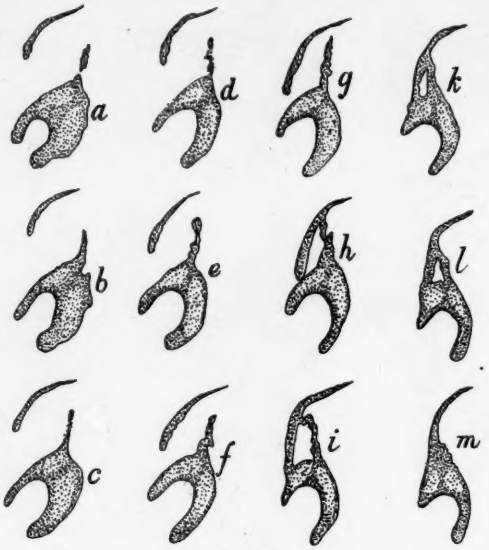


Fig. 62

to be retracted somewhat inwards by the attachment of the septum. In the present case this dimple—which I will distinguish in the sequel as *enamel-navel*—is but a shallow one.

After having demonstrated the occurrence of two centres of pulp-formation in the enamel-organ of human embryos, some examples may follow to prove that in other mammals the histogenetical differentiation proceeds in similar manner.

In fig. 62 a number of successive sections through the enamel-organ of $\bar{i}_2$ of a cow are drawn (series *A* of my collection). It is obvious that in this specimen the organ has still its enamel-niche, an indication of its rather early stage of development.

Furthermore it is not at all dubious that there are two points at which the transformation into pulp-mass is beginning, one in each half of the organ. They are separated from each other by the layer of undifferentiated cells, known already as enamel-septum. The enamel-niche has not yet been formed.

The latter formation was very well developed in the following case, drawn in fig. 63, which concerns the enamel-organ of $\bar{\imath}$ of a sheep (series *Z* of my collection). In the sheep the enamel-organs are directed in a somewhat unusual manner, the base being directed medially and the dental papilla pushing into it, from this side. There exists in this case—as commonly in the sheep—a very wide enamel-niche, with spacious aperture. The presence of two pulp-centres, separated by the septum also in this case is not subject to any doubt. In fig. 63 *e* a very fine enamel-navel is visible.

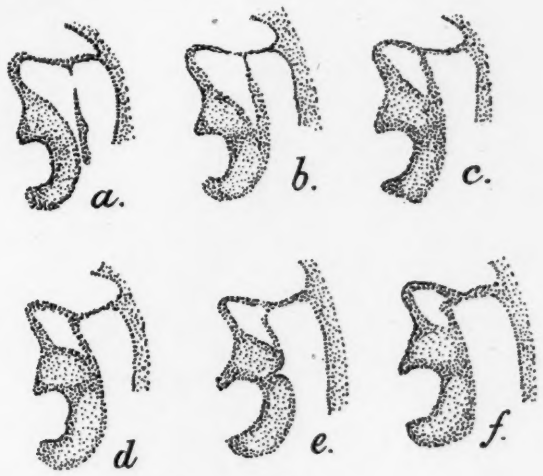


Fig. 63

That in Marsupials the genesis of the stellate reticulum does not differ from that in placental mammals is proved by fig. 64, representing four sections through the germ of an $\underline{m}_2$ of Dasyurus viverrinus (series *E* of my collection). In two of these sections the enamel-navel is also visible.

Finally fig. 65 shows the occurrence of a double pulp-centre in the enamel-organ of the horse. The drawings represent six sections through the germ of $\bar{\imath}_2$ of this animal (series *D* of my collection).

I think the correctness of my assertion that in mammals there are two centres of pulp-formation and not one single, to be sufficiently proved by the foregoing examples.

Now we will proceed to examine the further behaviour and development of the enamel-septum. In the first place we intend to inquire into the relation between the septum and the other components of the organ.

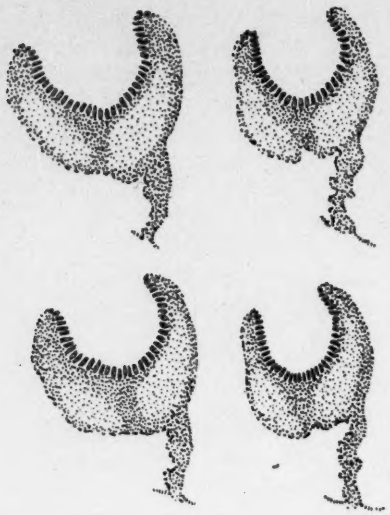


Fig. 64

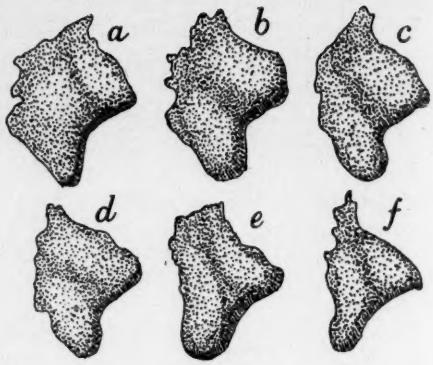


Fig. 65

The fact has already been mentioned that the cells of the septum keep their indifferent character. Now there exists still another layer in the organ which behaves in the same manner, namely the layer of intermediate cells. And in examining the relation between the septum and the layer in a much differentiated organ, the former appears on longitudinal sections as a conical outgrowth of the latter directed to the apex of the organ. This is demonstrated in figs. 66, 67, 68 and 69, showing sections through the enamel-organs of different mammals in which the relation between the septum and the layer of intermediate cells gradually becomes more evident. Moreover these figures

Fig. 66

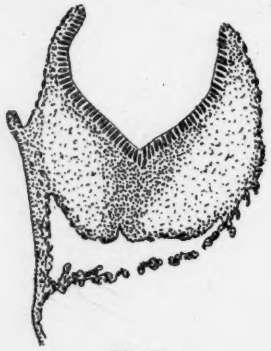


Fig. 67

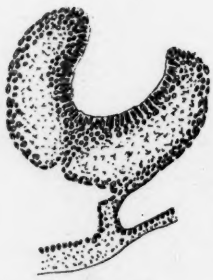


Fig. 68

Fig. 69

give an instructive survey of the histological differentiation of the septum. In fig. 66, showing a section through $\overline{m}_1$ of Mustela erminia there is not yet a clear difference between the elements of the pulp-masses and those of the septum; the centres are recognisable only by a lesser density of the nuclei, being evidently the cell-bodies somewhat swollen up. In fig. 67, representing a section through $\underline{m}_1$ of Hyrax syriacus the pulp-formation has proceeded further. Some stellate cells are to be recognised; already the layer of ameloblasts, as well as the superficial epithelium are recognisable without difficulty, while the layer of intermediate cells, covering the ameloblasts, has become sharply bounded. Now this layer prolongs itself into the middle of the organ as a broad partition wall, attaching at the top of the organ, where a well developed enamel-navel is visible.

A further stage of development is shown by fig. 68, representing a section through $\underline{m}_1$ of Canis familiaris (series *T* of my collection).

In both centres of pulp-formation the cells acquire the typical stellate form, the nuclei of the cells of the stratum intermedium are enlarged and the elements of the septum, extending through the organ from the stratum intermedium to the very well developed enamel-navel show quite the same character.

In fig. 69, representing a section through $\overline{m}_2$ of Macacus cynomolgus, a slight difference becomes visible. While the nuclei of the cells of the intermediate layer preserve their original more rounded form, those of the septum become more oblong, stretched out parallel to the axis of the organ.

The latter phenomenon I have observed but rarely. A very fine case of it I found in the molars of Bos taurus.

In a more advanced stage of development of these teeth, in which the internal differentiation of the organ was finished, the enamel-septum appears as formed by much elongated and flattened cells as may be seen in fig. 70, in which a section through $\overline{m}_2$ of Bos taurus (series *E*) is represented. One has, of course, the opportunity of observing an image as represented in fig. 70 only, when the section through the organ agrees with the direction in which the cells are lengthened. If such is not the case, the cells being cut through obliquely or transversely, appear in the section as rounded elements and seem to have preserved their original form.

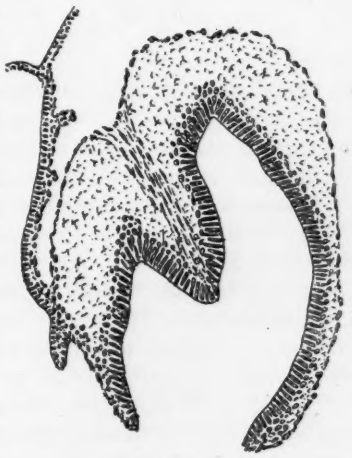


Fig. 70

On the evidence of fig. 70 we may arrive at the conclusion, that the elements of the septum during the further develop-

ment of the organ are not transformed into stellate cells: in this figure their form being already specialised so far in another direction, the possibility of transformation into stellate cells may be considered as wholly excluded.

The septum is not always as strongly developed as in the preceding examples. Sometimes it becomes very narrow, existing only as a double line of cells. A very instructive example of this condition is seen in fig. 71, in which a part of the organ of $\underline{i}_2$ of Propithecus diadema (series *A*), is represented much magnified. This figure may serve also to draw attention to a phenomenon in my opinion of no mean value with regard to the morphological and phylogenetical signification of the septum. On considering carefully the surface epithelium in fig. 71, one will note its failure at the spot where the septum is attached.

Fig. 71

The elements of this epithelium are characterised by the power to become stained very intensively. This fact facilitates the statement that this layer of external epithelium curves inwards to form the septum. The discontinuity of the covering epithelium in the navel of this enamel-organ was very obvious.

Corresponding phenomena may be observed in the enamel-organs of the molars of Marsupials, an example of which is given in fig. 72. This figure represents a section through an $\overline{m}_3$ of Dasyurus viverrinus (series *F*). The covering epithelium, forming a very deep navel, curves inwards to the layer of intermediate cells. The section drawn in fig. 72 resembles much that of a Macropus Cillardieri, figured by Hopewell Smith and Tims in the *Proc. Zool. Soc.*, London, 1911, Pl. XLVII, fig. 4, and described by the authors as follows: "Figure 4 shows the subdivision of an enamel-organ into two parts, by an epithelium septum passing from the outer enamel epithelium to the inner, where the latter lies over the apex of the dental papilla. This occurs in more

than one cheek-tooth and may be seen on both sides. We have never met with anything of the kind before. We can offer no other suggestion than that it is a double enamel-organ taking part in the formation of a single tooth."

Not without intention I intercalcate this quotation, because as will be pointed out in one of the next essays, I agree with the authors as to the interpretation of the appearance.

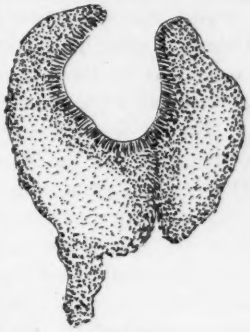


Fig. 72

I have once had the opportunity of observing a very particular function of the enamel-septum, which I will shortly mention. As to the question whether the enamel-organs are vascularised or not, the discussion is not yet closed. There are authors who assert that the organs contain no vessels at all, on the other hand there are investigators who state that a vascular network lies in the stratum intermedium. Personally I have failed to detect any vessel in the organ of mammals, except in one case. And the vascularity of the organ was in this case so obvious, that it seemed necessary to me to deal with my observation in a special paper (*Anatomischer Anzeiger*, vol. XLVIII. 1915). This communication concerns the enamel-organs of Phascolarctos cinereus, of which I have given in the above mentioned paper a series of illustrations, proving in an unquestionable manner the vascularity of these organs. In a somewhat advanced state of development the well-known stratum intermedium is lost in the enamel-organ, a very dense network of vessels covering the layer of ameloblastic cells. Now, in relation to the point discussed in the present paper it is very interesting to see in what manner the vessels enter the organ. This is illustrated by fig. 73, in which a part of a section through the organ of $\underline{T}_2$ of Phascolarctos is represented. The formation of dentine and enamel had commenced already, a thin layer of these hard tissues covered the apex of the dentinal papilla. Now fig. 73 shows how from the surrounding mesenchyme vessels enter into the enamel-organ by the way of the enamel-septum. To illustrate this fact I have chosen intentionally a section in which a vessel lies within the septum, while another in the navel of the organ is on the point of penetrating it.

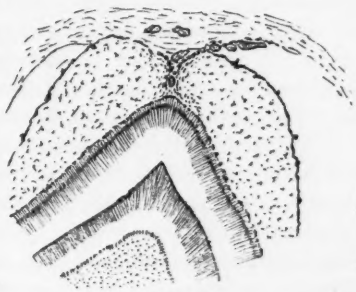


Fig. 73

As to the manner in which these vessels form the network in the enamel-organ, I refer the interested reader to my above-mentioned paper in the *Anatomischer Anzeiger*. For the present it was only my purpose to mention this particular function of the enamel-septum.

So far on the participation of the septum in the structure of the enamel-organ. Now we will go on in discussing its morphological and topographical particularities. The knowledge of these particularities will render intelligible the fact that this formation is nearly unknown in the odontological literature, though it may have been observed already by many embryologists, but not recognised by them in its real significance, and considered as an accidental appearance without any genetical importance.

The denomination of the formation as an enamel-septum or partition wall holds good only for the very first phase of development of the enamel-organ. Only in very young stages does the septum extend from the front to the back wall, entirely separating the two centres of pulp-formation from each other. Now concerning the relation between the septum and these two centres, it must be emphasised that the beginning in two spots of the transformation into reticular cells, is the essential point, the septum being only the necessary consequence of it. Nevertheless, the fact that the elements of the septum acquire in a further stage of development a typical specialised form, is to be appreciated as a hint that the septum has also a history of its own, and that it may not be considered exclusively as a consequence of the double centres of pulp-formation. This view is strengthened by the fact that rudiments of the septum are to be found even in enamel-organs in a very advanced stage of development.

The morphological history of the septum may be now summarised as follows.

It has already been mentioned that only in very young stages of development is the septum a real complete partition wall, dividing the inner mass of the enamel-organ in a lingual and buccal half. This state is a transitional one, for in the growing and increasing enamel-organ the two centres of pulp-formation soon fuse together in the anterior as well as in the posterior part of the organ, so that the septum, surrounded by reticular tissue becomes reduced to a central formation of conical form. This reduced form in which it is usually met with, may be considered as the main reason that it is scarcely known in literature, and that its original nature has not yet been recognised.

Intentionally I have laid much stress upon the original character of the formation as a real complete partition wall, dividing the organ into two halves. For after my first publication of it in the German language, Ahrens has expressed doubt about this assertion. He describes the formation as being not a septum, but, from the very beginning, a strand (emailstrang) running from the layer of intermediate cells to the top of the organ. The difference between our views is relatively of no importance, for the principal point—the fact that the pulp-formation does not begin in the centre of the organ—is accepted even by Ahrens whose view of the septum I have shown to be erroneous[1]. And truly the mentioned fact is of the greatest significance as to the morphological value of the enamel-organ, as will be demonstrated later on.

After being surrounded by reticular tissue the concentration of the septum

[1] "Ueber die Entstehung des Schmelzseptums," *Anat. Anzeiger*, vol. XLVIII. 1915.

to a conical strand progresses more and more. And when in somewhat older enamel-organs the level of the section runs obliquely with regard to the direction of the septum, the latter appears as a rounded heaping up of un-

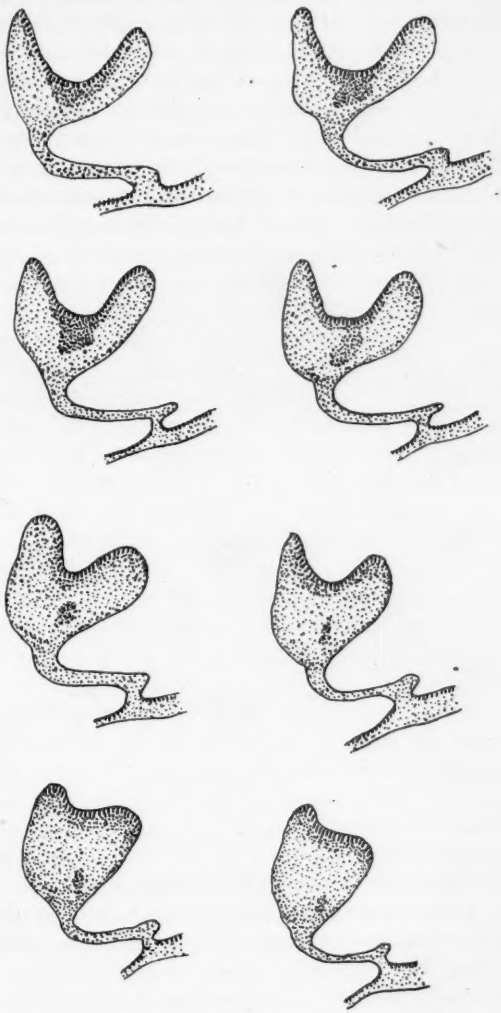


Fig. 74

differentiated cells, wholly enclosed by reticular cells. A very fine example of such a condition is given in fig. 74, showing eight sections through the organ of $\underline{m_2}$ of Macacus cynomolgus. It is obvious that the septum in this case is

reduced to a cylindrical strand, passing through the pulp-mass from the base to the top.

In this reduced form the septum is already known in literature, but not generally. The French histologist, Renaut, has given, as far as I am aware, the first short description of it[1] and calls it the "directing enamel-cone (cône adamantin directeur)," because he thought that this strand determined the direction in which the apex of the tooth will push through the enamel-organ. Now it is true that in monocuspidate teeth the septum—as I will continue to call it, even in its reduced strand-shape form—extends from the apex of the tooth to the outer epithelium at the top of the organ, as illustrated by the figs. 66, 67 and 68 for instance, and accordingly indicates the way which the pushing tooth shall take. This is, however, not an absolute necessity, as is proved by fig. 70, the septum terminating here, between the two cusps of the molar tooth.

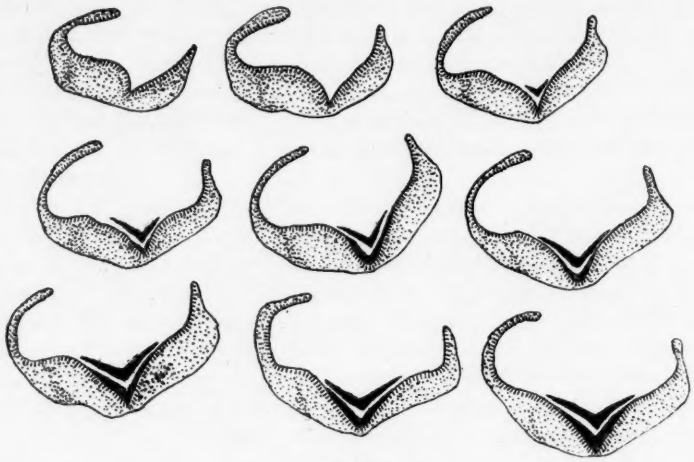


Fig. 75

It is obvious, furthermore, that, though in many cases the direction in which the tooth perforates the organ is indicated by the septum, this fact ought not to be taken into consideration in a discussion upon the significance of the septum. For it would be an error to take as subject of this discussion the septum in its reduced cylindrical shape, instead of in its original form as a real complete partition wall.

A conclusive proof that the enamel-septum is independent from the apex dentis and therefore unfit to accomplish the task of directing element is given in fig. 75, in which some sections are represented through the anterior part of the germ of $\underline{m_2}$ of Galeopithecus, on which the formation of enamel and dentine has already begun. The septum is situated in this specimen very eccentrically,

[1] *Traité d'histiologie pratique*, p. 248. Paris, 1897.

without any topographical relation with the apex of the tooth, which has nearly reached the outer epithelium of the enamel-organ.

Such an eccentric situation is met with very seldom and finally in fig. 76 there is reproduced yet another case of it, being a section through $\overline{m}_3$ of Chrysothrix sciurea.

Fig. 76

With this case I wish to finish the description of the enamel-septum. It is—as mentioned already—my intention to restrict myself in the present paper to the communication of my observations only, putting off the discussion upon their significance to one of the next essays. Yet it seems to me not wholly out of place to anticipate some general considerations.

A first remark concerns the septum. It is of great importance, as bearing on the significance of this formation, that it is met with exclusively in the enamel-organs of mammals. I have examined the genesis of the teeth in reptiles as thoroughly as that of mammals. And I have never seen in any enamel-organ of this group of vertebrates the smallest trace of an enamel-septum. It may be stated as a matter of fact that the septum is a formation typical of the teeth of the highest class of the vertebrates, and in some way or other its origin must be the consequence of the manner in which the teeth of the mammalia have taken origin from those of reptiles. For that the dentition of mammals must be derived from that of reptiles is no longer subject to any doubt, only as to the manner in which this evolution has taken place are the opinions of the authors not unanimous. A special essay will be devoted to my own views upon this subject.

Now one may remember that after my description of the external developmental appearances of the enamel-organ, I made the remark that the enamel-niche and canal fail in the tooth-genesis of reptiles, appearing exclusively during the development of mammalian teeth. And the conclusion at which I arrived was necessarily the same as that just given: the enamel-niche must be a result of the manner in which the evolution of the mammalian teeth took place. Therefore a relation must exist between the external developmental and the internal histogenetical phenomena, for both result from the same cause, and an attempt to solve the problem of the evolution of mammalian teeth must demonstrate at the same time the origin of the enamel-niche (canal) as well as that of the enamel-septum as a consequence of this process.

Now a very striking agreement between both phenomena may be pointed out here, by which a main morphological character of the mammalian enamel-organ comes to light.

Our researches have taught us, firstly, that in the tooth-genesis of mammals there is a common dental band from which two special bands emerge,

attaching themselves at the buccal and lingual sides respectively of the enamel-organ. In reptiles on the contrary, there is but one single connection between the organ and the dental lamina. This fact gives rise to the question whether the enamel-organ of the mammals is a single organ, or a compound one, being homologous with two organs of reptiles and not with a single one. If this point of view were true, the mammalian organ should be, so to say, a twin-organ, in which the constituent elements are situated as a buccal and a lingual one.

Now, this point of view is surely strengthened by our second observation, described in the present paper. We have demonstrated that in the organ of mammals there is not a single centre of pulp-formation, arising in the middle of the organ, but there are two centres, one in its buccal and one in its lingual half. This fact too is favourable to the appreciation of this organ as a double one, built up by two elementary organs, a buccal and lingual one.

I confine myself to throwing simply this light upon the morphological nature of the enamel-organ of mammals, the working out of this idea is to be put off to one of the next essays, after the exposition of some details on the origin of teeth in reptiles.

Yet I cannot end this essay without pointing out a consequence of the above view concerning the teeth. If, in reality, the mammalian enamel-organ be a compound one, the tooth itself also must be of the same nature, built up by two elements each homologous with a reptilian tooth. The buccal cusps of the mammalian tooth should represent then the one, and the lingual cusps the other reptilian tooth. The mammalian tooth should be then, what I will call a "dimer" tooth.

This consequence forms the fundamental point of my hypothesis upon the morphological value of the mammalian tooth and its relation to the teeth of reptiles.

THE PRIMORDIAL CRANIUM OF *TATUSIA NOVEMCINCTA* AS DETERMINED BY SECTIONS AND MODELS OF THE EMBRYOS OF 12 MILLIMETRE AND 17 MILLIMETRE C.R. LENGTH[1]

By Professor FAWCETT, M.D. (Edin.),
University of Bristol.

The embryos of which the crania are to be described were kindly given to me by Professor Wood Jones, and were cut into sections of 15 microns thick and stained with Mallory's triple connective tissue stain.

The 12 mm. stage will be described first.

THE PRIMORDIAL CRANIUM OF A 12 MM. *TATUSIA NOVEMCINCTA* EMBRYO
(Pls. VI, VII, VIII, IX)

Following the methods I have previously adopted in regard to the description of the primordial cranium, I will consider it here as consisting of the following parts. First a neural cranium, second a visceral cranium.

The osseous skeleton will be described separately.

The Neural Cranium may be divided into the following parts, viz.:

1. A central stem.
2. Appendages to the central stem.
3. Commissures which connect the central stem with the appendages.
4. Lateral structures.
5. Commissures connecting the lateral structures.
6. Dorsal structures, i.e. structures which lie dorsal to the encephalon and form a cartilaginous roof to the cavum cranii.

1. The Central Stem.

The central stem is at a very important morphological stage, because it shows three independent elements which are from behind forwards:

(*a*) The *pars chordalis.*

(*b*) The *pars trabecularis.*

(*c*) The *pars interorbito-nasalis.*

The condition recalls that of the mole at the 10–11 mm. stage in which similar cartilaginous elements are present and independent of one another (Noordenbos and Fawcett); but in Tatusia the independence of the pars

[1] The expenses of this research were to a large extent borne by the University of Bristol Colston Research Society.

trabecularis and pars interorbito-nasalis is maintained later than in the mole. The condition is of interest because it has hitherto been assumed that the nasal septum is formed by forward prolongation of the pars trabecularis. This is certainly not the case either in Tatusia or Talpa[1].

(*a*) *The pars chordalis.*

The pars chordalis is of considerable length and posteriorly of considerable breadth. In general form as viewed from above it is quadrilateral, but narrower in front than behind. It may be regarded then as having four borders which are anterior, posterior, and two lateral.

The posterior border is at least twice as wide as the anterior; it forms the anterior margin of the primary foramen magnum, is concave towards that foramen and the concavity is deepest at the middle line where a well-marked *incisura anterior* is formed in which the cartilaginous dens is lodged. The lateral limit of the posterior border may be taken as at an antero-posterior line drawn obliquely from within forwards and outwards through the medial margin of the hypoglossal canal.

The anterior border is narrow from side to side and concave forwards. Its extremities therefore project forwards towards the pars trabecularis from which it is separated by dense cellular tissue in which is lodged the *chorda dorsalis*.

The lateral borders are the longest and may be described as consisting of two parts, viz. a posterior and an anterior. The posterior part is somewhat shorter than the anterior part, and it forms the medial margin of a large space which will later become the *foramen jugulare*: the anterior part is in close relation with the medial side of the "cochlear" segment of the pars cochlearis of the auditory capsule, and it is in its whole length connected with this by a certain amount of cellular tissue. At a later stage this cellular tissue will in great part be replaced by cartilage, but a small vacuity will persist as the basi-cochlear fissure (Pl. X).

At the junction of the various borders with one another angles are found, thus, a postero-lateral angle lies at the junction of each lateral border with the outer end of the posterior border. This postero-lateral angle is directly continuous with the ex-occipital cartilage, the site of the continuity being perforated by the hypoglossal canal. At junction of the lateral borders with the anterior border antero-lateral angles are formed which form the horns of the crescentic anterior border of the pars chordalis.

The surfaces of the pars chordalis are superior or caval, and inferior. The superior surface is markedly concave from side to side, but near its anterior end this concavity is replaced by a transverse convexity under which the chorda dorsalis runs. Save at this spot the chorda dorsalis in its forward course from the dens lies on the caval surface of the pars chordalis.

The inferior surface is broad in its posterior half flattened or even slightly

[1] What I have termed pars trabecularis Noordenbos calls the *lamina polaris*. "Ueber die Entwickelung des Chondrocraniums der Säugetiere," *Petrus Camper*, vol. 3, 1906.

concave, but in its anterior half or so, it is narrow and convex from side to side and tends to project especially at its anterior half in the form of a keel.

(*b*) *The pars trabecularis.*

This element of the central stem is of comparatively small size and may be described as a pentahedral plate of cartilage perforated centrally by the hypophyseal duct. It is pointed anteriorly, straight posteriorly. Its borders are two antero-lateral, two lateral and one posterior.

The antero-lateral borders commence at the pointed anterior extremity, and diverge from one another rapidly as they are traced backwards. They form the postero-medial boundaries of the incomplete sphenoidal fissure.

Each lateral border is subtended by a mass of cellular tissue which is divisible into three parts, viz. an anterior which is continued out to the cartilaginous *ala temporalis*, an intermediate which is continued outwards in front of the foramen caroticum, then lateral to that foramen to fuse with the cochlear capsule, and is the primordium of the *anterior trabeculo-cochlear commissure*, a posterior which passes outwards behind the foramen caroticum as the posterior trabeculo-cochlear commissure to fuse with the cochlear capsule.

The posterior border is raised up to form a transverse crest which is the *crista transversa*.

The surfaces of the pars trabecularis are two in number, viz. a superior or caval, and an inferior. The superior surface is concave and at the deepest part of the concavity is perforated by the hypophyseal duct. The inferior surface is convex from side to side and marked in its middle by an antero-posterior keel-like ridge, which is perforated at its middle by the hypophyseal duct.

A large vacuity separates the pars trabecularis from the pars chordalis as viewed from below in the model, because the connective tissue has not there been modelled in order that the chorda dorsalis which makes a curious hook-like bend downwards into the vacuity may be brought into view.

(*c*) *The pars interorbito-nasalis.*

The pars interorbito-nasalis is separated from the pars trabecularis by a V-shaped fissure which laterally is confluent with the sphenoidal fissure of the corresponding side. The interorbital part of this segment of the central stem is very short and commences behind in a curious way. It looks, in fact, as if formed by the fusion of two common masses on each side of the middle line which have resulted from the junction of the pre- and post-optic limbs of the medial angle of the ala orbitalis, medial to the foramen opticum (Pl. VI). These two common masses fuse together at an acute angle and so seem to form the hinder part of the *inter-orbital septum*, viz. that part between the optic foramina; that part of the interorbital septum immediately in front of this fusion forms the medial boundary of the orbito-nasal fissure on each side of it. It is very low in height. The remainder of the pars interorbito-nasalis, which lies in front of the interorbital septum is the *septum nasi*.

The septum nasi consists of two parts, viz. a *subcerebral* and a *precerebral*. The subcerebral part has a superior or caval border which is comparatively thin and continued forwards in the plane of the floor of the cavum cranii. The inferior border (Pl. VII) is thicker and is continued forwards almost parallel with the upper border. It however does diverge somewhat from the upper border when traced forwards and as a result the septum nasi gradually deepens from behind forwards. The precerebral part of the septum nasi is characterised by the fact that it on each side gives off a lateral expansion which forms the roof of the corresponding narial passage, and is later continued downwards as the lateral wall of the nasal capsule. The inferior border as traced forwards gradually rises towards the superior border but soon runs straight forwards parallel with that border, so that a very obtuse angle is formed between the two segments of the inferior border of the precerebral segment of the septum nasi. On each side of the anterior segment of the inferior border of the precerebral segment of the inferior border lies an *anterior paraseptal cartilage*, which in great part and from behind forwards is separated from the septum nasi by a narrow fissure, the *septo-paraseptal fissure*, but in front of this fissure is directly continuous apparently with the septum. Each anterior paraseptal cartilage is connected by its inferior border and near its anterior end by a cellular *lamina transversalis anterior*, with the lateral wall of the nasal capsule. The anterior end of the septum nasi was not chondrified and has not been represented in the model.

2. Appendages to the Central Stem (Pls. VI, VII, VIII, IX).

These from behind forwards are:

(*a*) The ex-occipital cartilages.
(*b*) The auditory capsules.
(*c*) The alae temporales.
(*d*) The alae orbitales.
(*e*) The lateral nasal capsules.

(*a*) *The ex-occipital cartilages.*

Each ex-occipital cartilage is a massive bar which passes backwards and outwards from the corresponding postero-lateral angle of the pars chordalis of the central stem. It may be regarded as springing by an anterior and a posterior root between which the hypoglossal canal is enclosed. It runs outwards and backwards practically parallel with the pars canalicularis of the auditory capsule and comes to an end posteriorly at a level corresponding with that of the pars canalicularis. If cut across coronally it is seen to be triangular in section; one face of the triangle is directed forwards and upwards towards the infero-medial surface of the pars canalicularis of the auditory capsule. This face or surface is formed on the *lamina alaris* and is separated from the auditory capsule by the recessus supra alaris which medially is continuous with the foramen jugulare, and laterally opens out to the exterior.

At no point at this stage is there any direct connection between the ex-occipital cartilage and the pars canalicularis of the auditory capsule. Another face of the ex-occipital is directed towards the cavum cranii looking somewhat obliquely upwards and inwards, and its lower margin forms the lateral boundary of the incomplete primary foramen magnum. The remaining surface which is infero-lateral is concave, being overhung by the lamina alaris (Pl. VII).

(*b*) *The auditory capsules.*

These are of very great size and at the present stage lie more in the floor of the cavum cranii than in the lateral margin. Each may be divided into two primitive parts, viz. a more lateral which containing the semicircular canals is the *pars canalicularis*, and a more medial which is termed the *pars cochlearis*, and this latter is sub-divisible into a vestibular and a cochlear segment.

At this early stage the auditory capsule as a whole is naturally but imperfectly chondrified, the pars canalicularis as is usual being more perfectly chondrified than the pars cochlearis, which in fact is only chondrified at its antero-inferior and postero-medial parts.

The whole auditory capsule at this stage has a very isolated position and has no cartilaginous connection with any other region of the chondro cranium. It is connected with the central stem by connective tissue only, no part of which shows at this stage any sign of chondrification.

The pars canalicularis. This is the lateral part of the auditory capsule and so named because it contains the semicircular canals which determine to a large extent its form. Its lateral aspect forms part of the lateral surface of the neural chondro cranium, whereas antero-medially it is directly continued into the pars cochlearis.

As a whole the pars canalicularis presents for examination four free surfaces of which one is lateral, another is anterior, another supero-medial, and the remaining one infero-medial.

The *lateral* surface is most conveniently regarded as being triangular in shape with base forwards, and with apex opposite, forming the so-called cupula. The borders of this triangular lateral surface are anterior or basal, superior and inferior and will be considered before the surface itself is described.

The anterior or basal border is very slightly convex in the forward direction. It commences above at the superior basal angle, which may perhaps be the representative of a later-forming tegmen tympani, though such a structure cannot be recognised at the stage now being described. Below this basal angle a slight notch is met with which, because it is caused by the crus breve of the incus cartilage is called the fossa incudis. Some distance below and medial to the fossas incudis a slight projection (to which the, at this stage, cellular processus styloideus is attached) is found and is from the fact that the processus styloideus is attached to it, the *crista parotica*. Below this comes the inferior somewhat rounded basal angle which is the *processus mastoideus*.

The superior border commences anteriorly at the superior basal angle and

runs backwards and slightly downwards to the end of the cupula. From its anterior half there springs the *lamina parietalis*, a plate-like structure of which more will be said in the proper place. Behind the lamina parietalis the superior border is free and at this time forms part of the brim of the cranium. This part of the superior border is semi-cylindrical and caused by the superior or anterior semicircular canal and it forms part of the *prominentia semicircularis anterior*.

The *inferior* border commences at the inferior basal angle, passes backwards and upwards to the end of the cupula. It is semi-cylindrical and caused by the posterior semicircular canal, hence it is the *prominentia semicircularis posterior*.

The lateral surface—itself of triangular outline—is convex, and a special convex ridge runs across it from about the middle of the prominentia semicircularis posterior to the middle or thereabouts of the base. This ridge is the *prominentia semicircularis lateralis*, and is caused by the lateral semicircular canal.

The anterior surface is narrow from side to side, but deep in the vertical direction, it forms the posterior wall of the primary tympanic cavity. It is marked by the sulcus facialis which pursues a somewhat curved course along it, lying at first supero-medial then later as traced downwards more lateral. To the medial side of the lower end of the sulcus facialis a hollow is found which lodges the stapedius muscle and is therefore termed the *fossa musculi stapedii*.

The supero-medial surface looks more medialwards than upwards. It is bounded above by the prominentia semicircularis anterior, below by a semi-cylindrical elevation which is directed backwards and upwards towards the cupula and from the fact that it contains the crus commune of the semicircular canals (anterior and posterior) is the *prominentia cruris communis*. A small perforation exists in this prominence which is due to non-chondrification. It does not transmit anything and is filled with connective tissue. There is an anterior border to the supero-medial surface which at the same time forms the lateral margin of the meatus auditorius internus. At about the centre of the supero-medial surface a slight hollow is met with, which, because it is surmounted by the prominentia semicircularis anterior is termed the *fossa subarcuata anterior*. It is also termed the floccular fossa, but at this stage the flocculus does not rest in it; above and anterior to this fossa an elevation caused by the ampulla of the anterior semicircular canal is visible, and is indented by backward and outward extension of the upper lateral angle of the meatus auditorius internus. This elevation is the *prominentia utriculo ampullaris anterior*.

The *infero-medial* surface (Pl. VI) is of comparatively large size and concave in all directions. The concavity is not a deep one nor is it specially localised to one spot as, say, in the seal. It is the *fossa subarcuata posterior* and is bounded below and laterally to a certain extent by the *prominentia semicircularis*

posterior. Somewhat infero-anteriorly to the hollow a rounded prominence the *prominentia utriculo-ampullaris* marks the site of the ampulla of the posterior semicircular canal. The greater part of the infero-medial surface is directed towards the lamina alaris and it therefore forms the roof of the *recessus supra-alaris*, which medially is continuous with the foramen jugulare.

The pars cochlearis. The pars cochlearis is divisible into two parts, viz. "vestibular" and a "cochlear." The "vestibular" segment contains parts of the utricle and of the succule and corresponds roughly with the vestibule of the temporal bone. It is characterised at this stage mainly by the fact that medially it is perforated by the meatus auditorius internus and laterally by the *foramen vestibuli*, and by the fact that it is crossed superiorly by the facial nerve. At this stage it is in a very incomplete state of development, and the meatus auditorius internus is of enormous size owing to this incomplete chondrification; it is in fact so large that it practically takes up the whole of the medial or caval wall of the vestibular segment. Not only is the medial wall deficient but the roof of the upper wall of this segment likewise shows a great gap below the facial nerve, and there is therefore no cartilaginous sulcus facialis in this region. The inferior wall too of the vestibular segment is almost wholly occupied by the large conjoined foramina perilymphaticum and cochleae. The lateral wall is however more complete and is perforated by the comparatively small *foramen vestibuli* into which is fitted the foot of the *stapes* cartilage. This wall forms the upper part of the medial wall of the primitive tympanic cavity.

The "cochlear" segment of the pars cochlearis is only chondrified at this stage to a very slight extent at its infero-medial aspect, all the rest is in a dense cellular condition but it is of considerable size and is connected with the central stem in the manner already indicated above (see pars trabecularis). Its surfaces are supero-medial, antero-lateral and inferior. The supero-medial surface forms a considerable part of the floor of the posterior cranial fossa and is much flattened. Except at its postero-medial part this region is quite unchondrified and is represented in Plate VI stippled. The antero-lateral surface is in relation with the Gasserian ganglion and somewhat flattened, no chondrification is observable here. The inferior surface, which is markedly convex, is oval in form with its long axis directed from behind forwards and medialwards. It is crossed along its long axis by the internal carotid artery. At its hinder part the common foramen (foramina cochleae and perilymphaticum) is found, above which lies the *promontorium* caused by the initial part of the *ductus cochlearis*.

(*c*) *The alae temporales* (Pls. VI, VII).

Each ala temporalis is of very simple form being a mere curved rod of cartilage placed some distance below the plane of the general floor of the cavum cranii, and projected into the large *spheno-parietal* fontanelle partially dividing that fontanelle into an anterior segment which will become the sphenoidal fissure and a posterior segment, the *foramen pro-oticum* proper. Its medial

extremity is connected with the lateral border of the pars trabecularis of the central stem by connective tissue and from this medial extremity there projects in a downwards direction a short blunt process which is the *processus pterygoideus*. Amongst other structures the ophthalmic and maxillary divisions of the fifth nerve pass forwards above the ala temporalis to the cavity of the orbit. The mandibular division of the fifth nerve descends behind it.

(*d*) *The alae orbitales.*

These are exceedingly interesting in Tatusia. Each is a triangular plate which overhangs and forms the roof of the orbital cavity. Each consists of a body or main mass with a base which forms part of the cranial brim. By its basal angle important relations are established. Thus, the anterior basal angle is connected by a well chondrified bar with the frontal prominence of the pars intermedia of the paries nasi, the bar in question being the *sphenoethmoidal commissure*, which forms the lateral boundary of the *orbito-nasal fissure*. The posterior basal angle is joined by connective tissue only with the anterior extremity of the *lamina parietalis*, an important point in the phylogeny of the lamina parietalis. The apex of the ala orbitalis bifurcates into two long limbs which enclose and meet medial to the foramen opticum, a foramen which is of large size and oval in shape. Of these two limbs the anterior or preoptic is the more slender, each being cylindrical in form. Union between the two limbs having been established the common mass curves forwards and medialwards to join the corresponding postero-lateral part of the pars interorbito-nasalis, the appearance presented giving the impression that this pars interorbito-nasalis bifurcates when traced backwards. From about the middle of the ventral surface of the post-optic limb of the apex of the ala orbitalis a well marked process projects laterally. This gives attachment to the rectus system of muscles of the eyeball and is the *ala hypochiasmata* (Pl. VII). From the examination of a younger stage, viz. that of 10 mm. C.R. length it seems evident that the ala hypochiasmata chondrifies independently of the post-optic limb of the ala orbitalis and is to be considered as part of the pars interorbito-nasalis. In the body of the ala orbitalis somewhat lateral to the foramen opticum a small foramen is met with which transmits a blood vessel from the cavum cranii to the orbital cavity (I have queried this in Plate VII as foramen epiopticum).

(*e*) *The lateral nasal capsules.*

These structures will be described later under the nasal capsule.

3. Commissures connecting the Central Stem with the Appendages.

As these structures are all unchondrified their description will be deferred until the 17 mm. stage is described.

4. Lateral Structures.

These are in this case the lamina parietalis and the ala orbitalis. No supra-occipital cartilages are as yet chondrified.

The *lamina parietalis* is a plate-like cartilage which springs from the anterior half of the superior border of the pars canalicularis of the auditory capsule. Each is directed upwards and forwards for a short distance, it then turns wholly forwards arching over the spheno-parietal fontanelle and ends in close contact with the posterior basal angle of the ala orbitalis but is separated from it by a narrow interval filled by connective tissue.

The *ala orbitalis* having been previously fully dealt with need not further be described.

5. Lateral Commissures.

The only complete lateral commissures are the spheno-ethmoidal; the orbito-parietal commissures are not complete since the lamina parietalis is not fused with the posterior basal angle of the ala orbitalis.

The *spheno-ethmoidal* commissure (Pls. VI, VIII, IX) on each side is a strong bar well chondrified connecting the anterior basal angle of the ala orbitalis of its side with the frontal prominence of the pars intermedia of the paries nasi. It forms the lateral boundary of the orbito-nasal fissure.

The nasal capsule.

The nasal capsule is not perfectly chondrified at this stage, the anterior extremity being wholly in a cellular condition, only so much as consists of cartilage has been modelled. What is chondrified forms a relatively enormous structure which consists of a subcerebral and precerebral part.

When viewed from above it presents a pear-shaped form, the large bulbous end of the pear being posterior. So much as can be seen from the front consists then of a narrower anterior part, the *pars anterior* and a much wider though shorter posterior part, the *pars intermedia.* The *pars posterior* is seen from the caval aspect and it is to a certain extent overlapped by the alae orbitales, though separated from them by the orbito-nasal fissure.

The subcerebral part which forms the anterior part of the floor of the cavum cranii shows two large vacuities on each side of the septum nasi no lamina cribrosa having been developed at this stage; and the plane of the septal wall together with the upper margin of each lateral part of the nasal capsule is practically that of the floor of the cavum cranii generally, but the plane of the upper or dorsal surface of the precerebral part is almost at right angles with that of the subcerebral part (Pls. VIII, IX).

The precerebral part as seen from above and in front is almost complete save for a small foramen at the junction of the pars anterior and the pars intermedia. This foramen, the *foramen epiphaniale,* lies near the upper end of the sulcus *antero-lateralis* which separates the pars anterior from the pars intermedia. It transmits the lateral branch of the nasal nerve. In the middle

of the precerebral part an antero-posterior sulcus is seen—the *sulcus dorsalis nasi* and on each side of this lies a longitudinal antero-posterior semi-cylindrical elevation which is the roof of the corresponding narial passage.

The lateral wall (Pls. VIII, IX) of the nasal capsule is incomplete in front, but is divisible into a pars anterior, a pars intermedia and a pars posterior. The *pars anterior* is separated from the pars intermedia by a well-marked curved sulcus which commencing above and behind not far from the antero-lateral margin of the subcerebral part curves forwards then downwards and finally somewhat backwards towards the lower margin of the lateral wall (paries nasi). The sulcus is the *sulcus antero-lateralis*. It corresponds with the crista semicircularis on the medial surface of the lateral wall. The *pars intermedia* is separated from the pars posterior by the *sulcus lateralis posterior*, which commencing above opposite the attachment of the spheno-ethmoidal commissure to the nasal capsule curves downwards then somewhat backwards and finally forwards to reach the lower margin.

Considering these parts in detail and taking first the *pars anterior*, one notices that it is deeper behind than in front, that above it is continuous with the roof of the corresponding narial passage whilst below it is free but incurved to form the cartilaginous maxillo-turbinal; the *pars intermedia* is of great height and lateral projection. It is divisible at this stage into two well-marked subdivisions of which the upper part is the *prominentia frontalis* and gives attachment to the spheno-ethmoidal commissure; the lower prominence is the *prominentia maxillaris* and it as usual gives attachment at about its most prominent part to the inferior oblique muscle of the eyeball[1]. These prominences correspond with recesses on the medial side of the lateral wall, the frontal prominence with the *recessus frontalis*, the maxillary prominence with the *recessus maxillaris*; the *pars posterior*, which is separated from the pars intermedia by the sulcus lateralis posterior—a sulcus which corresponds with the line of attachment of the main root of the first primary ethmo-turbinal on the medial aspect of the lateral wall of the nasal capsule—is the smallest segment of the lateral wall. It is narrow from above downwards and curved backwards and inwards towards the septum nasi. Its hinder small end forms the cupula nasi posterior. Its upper border forms the lower or anterior boundary of the orbito-nasal fissure through which the nasal nerve gains the orbital cavity. Its lower border is free but is not sufficiently incurved posteriorly at this stage as to form a lamina transversalis posterior. The lateral surface of the pars posterior forms the antero-medial wall of the orbital cavity and is the *planum antorbitale*.

The *medial* aspect of the lateral wall of the nasal capsule is extremely simple at this stage. It is divisible into the same segments as the lateral aspect. Its pars anterior is sharply marked off posteriorly in its upper half by the crista semicircularis but in its lower half it is only separated from the pars

[1] Dotted lines leading back to a dotted circle (the eyeball) indicate the inferior oblique muscle (Pl. VIII).

intermedia by a low rounded ridge.—The lower margin of the pars anterior is incurved to form the *maxillo-turbinale*, and at its anterior end the margin is much inbent and continued towards the anterior paraseptal cartilage by a connective tissue representative of the lamina transversalis anterior. The pars intermedia is deeply recessed and bounded posteriorly by the first *primary ethmo-turbinal*, which stretches from the upper to the lower margin of the medial aspect of the lateral wall and so cuts the pars intermedia completely off from the pars posterior. The cavity of the pars intermedia may be divided into an upper and a lower recess, the upper being the *recessus frontalis* which produces the prominentia frontalis on the exterior, the lower being the *recessus maxillaris* which produces the prominentia maxillaris on the exterior, there is no visible line of separation between these two recesses at this stage. In the anterior part of the recessus maxillaris the lateral nasal gland is lodged. The *pars posterior* is the smallest segment of the region under consideration. It lies behind the first primary ethmo-turbinal. No lamina transversalis posterior is developed at the present time. As regards the first primary ethmo-turbinal, it may be described as a triangular plate which projects inwards and forwards towards the septum and crista semicircularis; by its base it is attached to the entire depth of the medial aspect of the lateral wall, and its line of attachment corresponds with the sulcus lateralis posterior on the exterior. Its apex is free and turned forwards towards the crista semicircularis. The septum nasi has already been described (see pars interorbito-nasalis). The solum nasi at this stage save for the connective tissue lamina transversalis anterior is entirely wanting, but it is interesting to note that the connective tissue lamina transversalis anterior is upcurved about its middle to form an *atrio-turbinal*.

6. The Visceral Cartilages (Pls. VIII, IX).

These from before backwards are arranged in five pairs corresponding with five visceral arches.

The cartilaginous skeleton of the first arch is represented from behind forwards by the *incus* cartilage, the *malleus* cartilage and by Meckel's cartilage. The *incus* cartilage is remarkable for its great size. It consists of a relatively small body which is keyed into the back of the head of the malleus cartilage and projects upwards slightly above the latter as a small somewhat conical knob. The crura which arise from this body are of unusual length, the *crus posterior* or *breve* is of great length and runs almost straight backwards to reach the fossa incudis to the outer side of the basal border of the lateral surface of the pars canalicularis of the auditory capsule. The *crus anterior* or *longum* descends parallel with the manubrium mallei and is also of great length, to the medial side of its lower end the stapes cartilage is attached by dense connective tissue. This crus is at its lower part separated from the manubrium mallei by the chorda tympani nerve.

The *malleus* cartilage is remarkable for the small size of its head and very large size of its manubrium. The head articulates behind with the body of the

incus cartilage and sends outwards a considerable wing-like expansion to the front and lateral aspect of the body of the incus. The manubrium is very long and incurved at its lower end; along the medial side of its upper half the chorda tympani nerve ascends.

Meckel's cartilage starts from the body of the malleus cartilage and runs forwards as a simple cylindrical rod almost parallel with the plane of the precerebral plane of the dorsum nasi; at about the middle of its course it bends somewhat sharply medialwards then runs forwards gradually converging on its fellow, but as it is not completely chondrified at this stage it does not meet its fellow in the middle line.

The cartilages of the *second* arch are from behind forwards the stapes and the hyoid cartilage (Richert's). The stapes cartilage is comparatively small, is perforated by a stapedial artery and by its foot fitted into the foramen vestibuli; by its opposite extremity it is connected with the crus longnum of the incus by dense cellular tissue, and it still retains a connective tissue connection (interhyale) with the hyoid cartilage. The hyoid cartilage springs from the crista parotica of the pars canalicularis by connective tissue (latero-hyal), around whose lateral aspect the facial nerve winds, soon becoming cartilaginous it continues as such towards the middle line which it does not quite reach, as it suddenly bends downwards to articulate with the top of the anterior extremity of the thyro-hyal, and with the corpus hyale or basi-branchial of Parker.

The cartilaginous part of this rod shows no sign of segmentation.

The cartilage of the *third* arch—thyro-hyal—is comparatively short and lies in a plane almost parallel with that of the under surface of the main part of the neural cranium; from behind where it commences in a pointed extremity it is directed medialwards and ends not far from the middle line by articulating above with the hyoid cartilage, and in front with the corpus hyale. The cartilage to which I have referred as the corpus hyale is of small size and when viewed from the front triangular in shape, its base being downwards. By its lateral margins it articulates with the hyoid cartilage and with the thyro-hyal.

The cartilage of the *fourth* arch, viz. the thyroid cartilage is of great interest at this stage, lying in its hinder two-thirds in a plane parallel with that of the thyro-hyal and being of considerable depth it suddenly contracts owing to a deep notch which indents its upper margin and having suddenly harrowed it bends upwards to reach a plane posterior to the corpus hyale and there fuse with its fellow in the middle line. At a later stage the deep notch in the upper border becomes closed over from above and a comparatively large foramen takes its place (Pl. XIII). There is no cartilaginous connection at this stage between the thyro-hyal and the thyroid cartilage.

The cartilage of the *fifth* arch is represented by the cricoid which presents the usual form, save that the ring is not chondrified in front and medially.

The arytenoid cartilages are not yet chondrified.

7. The Osseous Skeleton (Pl. IX).

This at this stage is in an extremely simple condition, only two bones having appeared, viz. the maxilla and the mandible.

The *mandibula* is a large splint-like membrane bone placed lateral to the anterior half of Meckel's cartilage. It shows no sign of condyle or alveolar processes at this stage.

The *os maxillare* has just commenced to ossify, and is placed some distance behind the inferior margin of the pars anterior of the nasal capsule.

It is a tribute to the value of Mallory's connective tissue stain that one is able to model the maxilla at this early stage. Mall, who spoke disparagingly of stains as a means of detecting bone at early stages cannot have used Mallory's stain for that purpose, for in my experience the very finest spicules of bone are brought out by it. I agree that the commonly used haemaloxylin and eosin stain is very unreliable in such matters.

THE PRIMORDIAL CRANIUM OF THE 17 MM. C.R. STAGE OF *TATUSIA NOVEMCINCTA* (Pls. X, XI, XII, XIII, XIV, XV)

At this stage the chondro cranium has become much more complete, especially in regard to the following regions and structures. A well chondrified and large supra-occipital cartilage is present, which is fused with its fellow dorsal to the cavum cranii to form a large tectum cranii posterius, which additionally is fused with the ex-occipital cartilage of its side, and with the lamina parietalis. The auditory capsule has become more or less elaborated and is now definitely fused with the central stem by the three usual commissures, viz. chordo-cochlear, anterior and posterior trabeculo-cochlear. Between the posterior trabeculo-cochlear commissure and the chordo-cochlear commissure a small basi-cochlear fenestra persists. The meatus auditorius internus has become divided by a crista falciformis into an upper and lower part respectively foramen acusticum superius and foramen acusticum inferius, but the foramen acusticum superius is only complete so far as concerns the nerves for the ampullae of the anterior and lateral semicircular canals, the utricle and the upper nerve to the saccule. There is no foramen faciale, the facial nerve leaving the skull by a sulcus facialis on the upper part of the "vestibular" segment of the auditory capsule.

The fossa subarcuata anterior interna is reduced in size till it is a narrow deep pit which leads into the interior of the pars canalicularis. A well marked tegmen tympani is present.

The ala temporalis now appears fused with the middle of the anterior surface of the anterior trabeculo-cochlear commissure.

The pars trabecularis as viewed from the caval aspect is continuously fused with the pars chordalis of the central stem, but when viewed from below a large transverse gap separated them, the gap being occupied by the down-turned chorda dorsalis. The pars trabecularis however still retains its inde-

pendence of the pars interorbito-nasalis. Its cranio-pharyngeal canal has closed up. The alae orbitales whilst very generally retaining the form shown at the 12 mm. stage, have made some advances. Thus the post-optic limbs have sent backwards an anterior clinoid process. The pre-optic limbs have developed on the medio-anterior wall of the optic foramen a small spur for the attachment of the obliquus superior of the eyeball, and the optic foramen has become relatively reduced in size. The posterior basal angle has fused with the lamina parietalis forming now a continuous orbito-parietal commissure. The foramen lateral to the foramen opticum observed at the 12 mm. stage has increased in size (may it represent the foramen epiopticum of reptiles?).

Perhaps the most striking changes are observable in regard to the nasal capsule, which though as yet not completely chondrified is of enormous size—especially in length. The actual length of the pars interorbito-nasalis in the model amounts to 13 inches, whilst the length of the pars trabecularis and pars chordalis combined amounts to only 6½ inches. A cupula posterior with tectum nasi completum posterius is now developed, a lamina transversalis posterior is well chondrified, an anterior and a posterior paraseptal cartilage are present. The lamina transversalis anterior although not yet chondrified is easily made out and the medial aspect of the lateral wall of the nasal capsule has much increased in complexity mainly however by increased growth of the parts seen in it at the 12 mm. stage, very little in the way of new structure having appeared. No cartilaginous lamina cribrosa is as yet developed.

In the visceral chondro cranium certain advances have been made. Both the incus and the malleus cartilages are of enormous size and the crus posterior (breve) of the former lies as before on the lateral aspect of the lateral surface of the pars canalicularis of the auditory capsule. Meckel's cartilages have been fused together at their anterior extremities. The hyoid cartilage has had segmented off from it anteriorly a definite cerato-hyal, which at 12 mm. stage was directly continuous with the root of the hyoid cartilage. The thyro-hyals have now come into contact with the posterior margin of the ala of the thyroid cartilage but are still unfused with it. The deep notch in the upper margin of the ala of the thyroid cartilage is now converted into a foramen.

The osseous skeleton has naturally made considerable advance.

The two bones—*mandibula* and *maxilla*—have grown considerably, the mandibula being of great length and covering the greater part of the Meckel's cartilage laterally and reaching almost from the malleus posteriorly to the anterior fused ends of Meckel's cartilage. The maxilla seems to have ossified from two centres, a more medial which covers the lateral aspect of the maxillo-turbinal cartilage and a more lateral covering the prominentia maxillaris of the pars intermedia of the nasal capsule.

The *incisivum* is only represented by a small splint-like centre which lies on the medial aspect of the anterior end of the anterior paraseptal cartilage and which may be called the pars paraseptalis of the incivisum (Broom's "Pre-vomer").

The *zygomaticum* is present lateral to the processus coronoideus of the mandibula and a palatinum lies below the pars posterior of the nasal capsule. Finally a well developed frontale covers the postero-lateral aspect of the prominentia frontalis of the pars intermedia of the nasal capsule, and is continued backwards along the outer side of the orbito-parietal commissure for a considerable distance.

The *vomer* is not yet ossified but its primordium is easily recognised occupying its usual position, i.e. at the medial aspect of the hinder end of the anterior paraseptal cartilage as well as at the medial aspect of the anterior end of the posterior paraseptal cartilage (Pl. XV).

We may now consider in more detail the primordial cranium of the 17 mm. stage taking first the

1. Central Stem (Pls. X, XI).

This consists of the usual parts from behind forwards, viz. the pars chordalis, the pars trabecularis and the pars interorbito-nasalis. Of these parts the pars interorbito-nasalis is almost twice as long as the other two taken together. As viewed from the caval aspect the pars cochlearis and the pars trabecularis are completely fused with one another, but a glance at the inferior surface shows that this fusion is entirely at the upper aspect as a large transverse gap is visible from below between the two containing the chorda dorsalis. This gap although transverse to the long axis of the central stem is seen to run obliquely backwards so that if continued through into the cavum cranii it would appear at the anterior margin of the basi-cochlear fenestra which is the usual position. This obliquity suggests that during the mutual growth of the pars trabecularis and the pars chordalis the former has been thrust back over the latter and the crumpled up condition of the chorda dorsalis which occupies this gap supports this view.

(*a*) *The pars chordalis* (Pls. X, XI).

The pars chordalis stretches from the anterior margin of the foramen magnum to the afore-mentioned gap below or to an imaginary transverse line drawn through the anterior margin of the basi-cochlear fissures—or even, perhaps, a little in front of this. It is a quadrilateral plate whose antero-lateral angles fuse with the posterior trabeculo-cochlear commissures, whose postero-lateral angles are continued outwards beyond the hypoglossal canals to become the ex-occipital cartilages. The borders are anterior, posterior and lateral. The anterior border is narrow and only visible as such from below where it forms the posterior boundary of the *chorda-trabecular fissure*. The posterior boundary is deeply concave and at the deepest part of its concavity forms the *incisura anterior* which lodges the dens of the axis cartilage. This border forms the anterior boundary of the foramen magnum.

Each lateral border may be traced from the postero-lateral angle, i.e. to the anterior part of the basi-cochlear fissure. It may be divided into three parts, viz. a posterior, an intermediate and an anterior. The posterior part is

free and forms the medial boundary of the foramen jugulare. It is directed from behind forwards and medialwards. The intermediate part of the lateral border is fused with the pars cochlearis of the auditory capsule to form the *chordo-cochlear commissure*, and this commissure is of great antero-posterior width. The anterior segment of the lateral boundary is the shortest. It is free and forms the medial boundary of the basi-cochlear fissure.

The surfaces of the pars chordalis are superior or caval, and inferior. The superior or caval surface is wider behind than in front and is concave from side to side and the chorda dorsalis rests on almost the whole length of this surface in the middle line from before backwards, only sinking through to the under aspect at the anterior limit of the upper surface of the pars chordalis. The inferior surface is wide posteriorly, narrow interiorly. It is convex from side to side, but from end to end shows a concavity under its broad part. The under aspect of the narrow anterior segment projects downwards almost keel-like. In front of this keel-like projection the chordo-trabecular fissure is seen to contain the downbent anterior end of the chorda dorsalis.

(*b*) *The pars trabecularis.*

The pars trabecularis at this stage retains to a considerable extent its independence. As already mentioned, as viewed inferiorly the chordo-trabecular fissure (remnant of the basi-cranial fenestra) marks it off from the pars chordalis whilst anteriorly it is quite independent as yet of the pars interorbito-nasalis whether viewed from above or below. As in the younger stage described above it is of pentahedral form, pointed anteriorly where it juts into the notch at the back of the pars interorbito-nasalis, straight behind where confluent above with the anterior margin of the pars chordalis. Its borders are two antero-lateral, two lateral and one posterior. The antero-lateral borders are free and separated from the neighbouring hinder edges of the post-optic limbs (? alae hypochiasmatae) of the alae orbitales by a narrow fissure. The lateral borders give attachment from before backwards to the alae temporales, the anterior and posterior trabeculo-cochlear commissures, between which two latter the foramen caroticum is found. The posterior trabeculo-cochlear commissure is of great antero-posterior width. The posterior border of the pars trabecularis is only free as viewed from below and then only medially where it forms the anterior boundary of the chordo-trabecular fissure. The surfaces are caval or superior, and inferior. The caval surface is slightly concave from side to side and lodges the hypophysis. There is nothing bounding it behind which one could call a crista transversa, and there is no cranio-pharyngeal canal at this stage. The hypophysis is of small size. The inferior surface is markedly convex from side to side, and marked by a keel-like median antero-posterior ridge which is deeper behind than in front.

(*c*) *The pars interorbito-nasalis.*

This region and structure is of enormous length, being in actual measurement of the model 13 inches in length—and almost twice as long as the com-

bined partes trabecularis and chordalis. Comparatively low in height so long as it lies between the optic foramina which it separates, it suddenly increases in height between the orbito-nasal fissures which it also separates (Pl. XV). From this point onwards as nasal septum it consists of a subcerebral and a precerebral part and its height varies very little, perhaps it is greatest just behind the junction of the subcerebral and precerebral segments where its upper border is thickened to form a *crista galli*, from this region forwards there is a very slight fall in height, but there is a sudden increase in height at about the junction of the anterior and middle thirds of the precerebral parts. This increase is however more apparent than real as it is here that the processus lateralis ventrales are given off, and as they descend almost in the same vertical plane as the septum nasi the apparent depth or height of the septum is much diminished. More will be said regarding the septum nasi when the nasal capsule is described.

2. Appendages to the Central Stem.

(*a*) *The ex-occipital cartilages.*

In general form and direction these cartilages have changed but little on becoming older, but each cartilage at its posterior extremity is now almost completely fused with the neighbouring supra-occipital cartilage, slight notches median and lateral only remaining to indicate the site of their original separation (Pls. XII, XIII). Each ex-occipital cartilage leaves the corresponding postero-lateral angle of the pars chordalis by two roots which embrace the hypoglossal canal, each passes, at first backwards and outwards, lying parallel almost with the infero-medial surface of the pars canalicularis of the auditory capsule from which it is separated by the recessus and fissura supra-alaris, then it turns suddenly upwards by the side of the foramen magnum of whose lateral margin it forms a considerable part. It ends by fusing with the postero-lateral angle of the supra-occipital cartilage. The first stage is thick and strong and triangular in section. Its surfaces are, supero-medial, antero-lateral and inferior. The supero-medial surface is directed towards the foramen magnum and the cavum cranii. The antero-lateral surface is triangular in shape, is formed on the lamina alaris whose apex juts forwards under the pars canalicularis. The inferior surface is concave owing to the forward curve of the lamina alaris. Upon the anterior-lateral surface of the lamina alaris rest the sinus venosus transversus and the ganglia of the vagus and glossopharyngeal nerves.

(*b*) *The auditory capsules* (Pls. X, XI, XII, XIII).

These are of a very large relative size—and divisible into the two main parts, viz. pars cochlearis and pars canalicularis of which the former is subdivisible into vestibular and cochlear segments. Although by no means completely chondrified considerable advance has been made in that direction.

The cochlear part of the pars cochlearis is practically fully chondrified and is now attached to the central stem by three cartilaginous commissures which

are from before backwards, the anterior trabeculo-cochlear, the posterior trabeculo-cochlear and the chordo-cochlear. The two latter are of great antero-posterior width, hence the basi-cochlear fissure which lies between them is of small antero-posterior length.

The vestibular segment of the pars cochlearis is not yet completely chondrified but the meatus auditorius internus is now divided by the crista falciformis into a small foramen acusticum superius and a large foramen acusticum inferius. There is no commissura supra-facialis so that a facial canal is not present and the facial nerve rests in a sulcus facialis whose floor is only imperfectly chondrified and as a result opens into the foramen acusticum superius. The foramina cochleae and perilymphaticum are still unseparated from one another.

The pars canalicularis now shows a well-developed tegmen tympani which projects forwards over the incus-malleus joint. The fossa subarcuata interna is small in area but very deep, being at this stage a foramen opening into the interior of the pars canalicularis.

There is a fossa subarcuata on the infero-medial surface which likewise has an imperfectly chondrified floor. The foramen endo-lymphaticum is of large size and leads backwards into a long groove which lodges the ductus endo-lymphaticus after its exit from the foramen. These are the main points of distinction between this stage and that at 12 mm., and as the former has been fully described, no more detailed description of this stage is necessary so far as it concerns the auditory capsule.

(*c*) *The ala temporalis* (Pls. X, XI).

This cartilage still retains a simple form but is now united by cartilage both to the lateral border of the pars trabecularis and the anterior surface of the anterior trabeculo-cochlear commissure from which it passes laterally then makes a curve convex forwards, outwards, upwards, and backwards to end in a blunt point. In the concavity the mandibular division of the fifth nerve lies.

(*d*) *The ala orbitalis.*

The ala orbitalis shows a few growth changes, but retains to a large extent its form of the 12 mm. stage. The post-optic limb of the apical angle has developed a backwardly projected process (Pl. X) which has all the appearances of an anterior clinoid process, and the pre-optic limb sends backwards towards the medial side of the foramen opticum a small triangular spur from which the musculus obliquus superior takes origin. The foramen opticum has become relatively smaller than at its 12 mm. stage, but what I have ventured to call the foramen epiopticum is of larger size. The posterior basal angle is now completely fused with the anterior limb of the lamina parietalis so that a complete orbito-parietal commissure is formed. The anterior basal angle is as it was at the 12 mm. stage fused with the prominentia frontalis of the pars intermedia of the nasal capsule forming the spheno-ethmoidal commissure. The foramen epiopticum is well shown at this stage.

3. Lateral Structures.

These from behind forwards are the supra-occipital cartilage, the parietal plate, the ala orbitalis and the commissures which bind these lateral structures together.

The *supra-occipital cartilage*, which is now fused below with the upper end of the ex-occipital, is triangular in form, with base upwards (Pls. XII, XIII).

By its apex it is fused with the ex-occipital, by its anterior-basal angle it is joined to the parietal plate through what I shall term the *occipito-parietal commissure* and by its posterior or internal basal angle it joins that of the opposite cartilage to form the tectum cranii posterius vel synoticum.

The *parietal plate* is a somewhat quadrilateral curved plate of cartilage attached by its lower border to the anterior half of the upper border of the pars canalicularis of the auditory capsule. Its anterior border is continued to and fused with the posterior basal angle of the ala orbitalis under the designation *orbito-parietal commissure*. Its posterior border is joined by the supra-occipital cartilage as the occipito-parietal commissure. The upper border is free and forms part of the free upper lateral margin of the cranial cavity.

It may be well to say that for the most part the terms anterior and posterior borders of the parietal plate are artificial or imaginary borders drawn from the anterior and posterior limits of the spring of the plate from the auditory capsule.

The *ala orbitalis* has already been described.

The commissures are occipito-parietal, orbito-parietal and spheno-ethmoidal (orbito-nasal).

The occipito-parietal is the anterior attenuated basal angle of the supra-occipital cartilage which, arching forwards over the upper margin of the pars canalicularis of the auditory capsule and separated therefrom by the anterior part of the common *occipito capsular fissure*, joins the parietal plate.

The orbito-parietal commissure which connects together the parietal plate and the posterior basal angle of the ala orbitalis is an important site of origin of the musculus temporalis. It forms at this time the outer boundary of the spheno-parietal fontanelle and developmentally is a forward growth of the parietal plate to the posterior basal angle of the ala orbitalis as was seen in the stage previously described.

The orbito-nasal (spheno-ethmoidal) commissure has a twofold origin, viz. from the anterior basal angle of the ala orbitalis and a backwardly directed process from the prominentia frontalis of the pars intermedia of the auditory capsule. It bounds the orbito-nasal fissure laterally.

The *tectum cranii posterius* is of considerable size and is formed by the fusion of the medial basal angles of the supraoccipital cartilages of the two sides with one another. It is deepest centrally and it forms the hinder (upper) boundary of the primary foramen magnum.

The nasal capsule.

This truly enormous structure is as long as the remainder of the chondro cranium. It consists of the usual parts, viz. a septum, a roof, a lateral wall and a floor.

The septum nasi is that part of the pars interorbito-nasalis of the central stem which is included within the nasal capsule. It consists of two parts, viz. a subcerebral and a precerebral. The subcerebral part is of large size or perhaps one had better say of great length, almost equal in fact to the length of the precerebral part. It is almost uniform in height, but is a little higher at a short distance from the front than behind. This augmentation is the crista galli. Its superior margin separates the two subcerebral vacuities of the nasal capsule from one another, and there is as yet no sign of any lamina cribrosa. The inferior margin of the septum is much thicker than the superior, and it is especially thick posteriorly. Infero-lateral to its subcerebral part is on each side a *posterior paraseptal* cartilage. This is separated by a narrow *septo-paraseptal fissure* from the septum nasi. The precerebral part of the septum, like the subcerebral, may be described as having a superior and an inferior margin. The superior margin does not however project freely, or at all events it is connected directly with the lateral nasal capsule by the tectum nasi anterius. In its posterior half this part of the upper border may be said to be flush with the superior surface of the tectum nasi (Pl. X), but in its anterior half it is sunk below the level of the tectum at the bottom of the *sulcus dorsalis*.

The inferior border is thicker than the superior one and is convex from side to side. It has on each side of it in the greater part of its extent the anterior paraseptal cartilages which are separated by a narrow septo-paraseptal fissure from the septum; more anteriorly, i.e. is near the anterior end of the lower margin of this segment of the septum, the lamina transversalis anterior passes directly outwards from the septum to the lateral wall. This lamina, which will be described in detail later, may here be said to be continuous by its hinder border with the anterior paraseptal cartilage of its side, and in front with the processus lateralis ventralis (Pl. XIV). The main mass of the septum is for the most part of uniform thickness save near its anterior end. Here it greatly thickens below the level of the tectum anterius, a condition which is like that in mole, hedgehog, and in Miniopterus, forming the basis of a septo-turbinal. There is no septal foramen, and the anterior border of the septum is an oblique one, looking downwards and backwards.

The *roof* (tectum nasi) consists of two parts, viz. a tectum posterius and a tectum anterius. At this stage no lamina cribrosa is developed so that the subcerebral part of the roof is represented only by the tectum nasi posterius which is the forwardly curved dorsal part of the cupula nasi. This tectum posterius is at this stage quite free of the upper margin of the septum. Although the lamina cribrosa is not present, and although the cribro-ethmoidal crest is likewise absent, the olfactory nerves can be seen to leave the interior of the

nasal capsule in the usual arrangement, viz. an antero-lateral and a postero-median group. The antero-lateral supply especially the interior of the recessus frontalis of the pars intermedia, whilst the postero-median supply the septum and the interior of the pars posterior. From the anterior part of the recessus frontalis a *cribro-ethmoidal canal* runs forwards through the tectum anterius and ends at the *foramen epiphaniale.*

The precerebral part of the roof (Tectum nasi anterius) is long, broad and convex on each side of the septum. It may be said to be wider in front than behind, flat behind, but in front longitudinally grooved in the middle, the groove being the sulcus dorsalis nasi. Laterally the tactum runs more abruptly than usual into the lateral wall of the capsule, anteriorly the tectum forms a very slight projection—the spina cupularis.

The *lateral wall* (*paries nasi*) (Pls. XII, XIII) is divisible into three parts which are from behind forwards, the pars posterior pars intermedia and pars anterior. The pars posterior is separated from the pars intermedia by the *sulcus postero-lateralis*, the pars anterior is separated from the pars intermedia by the *sulcus antero-lateralis*. The sulcus postero-lateralis commences above at about the middle of the lateral boundary of the olfactory vacuity in the subcerebral segment of the nasal capsule, it descends to the inferior margin of the paries nasi after running a course convex backwards. Its upper end perhaps may be more precisely stated as at the hind edge of the attachment of the spheno-ethmoidal commissure.

The antero-lateral sulcus is very well marked. It commences above at a deep depression into which opens the anterior (external) orifice of the foramen epiphaniale. It descends with a curved course convex forwards and ultimately bifurcates to enclose a triangular area which corresponds externally with the recessus glandularis internally, the two limbs of bifurcation can be traced to the lower margin of the paries nasi. These two sulci which are such important external landmarks are of equal importance with reference to the medial aspect as they correspond with projections on the medial aspect of the lateral wall, thus the antero-lateral sulcus corresponds with the crista semicircularis and the postero-lateral with the first primary ethmo-turbinal.

The *pars posterior*, that part of the paries nasi which lies behind the postero-lateral sulcus is, as seen from the side, triangular in form with base forwards at the sulcus lateralis posterior. The apex is directed backwards towards the taenia preoptica of the ala orbitalis and separated from it by the orbito-nasal fissure. This apical region can be traced medialwards towards the septum nasi, but it is not fused therewith. The upper border of the pars posterior ends freely as the lateral margin of the subcerebral olfactory vacuity (Pl. X). The inferior margin is curved medially and takes a large part in the formation of the *lamina transversalis posterior*, but that part of it which lies anterior to the lamina transversalis posterior ends freely and helps to bound laterally the fenestra basalis of the solum nasi (Pl. XI).

The *pars intermedia*, as seen from the lateral aspect, is very large and

prominent. It consists of at least three parts, viz. a superior to which is attached the spheno-ethmoidal or orbito-nasal commissure, the *prominentia frontalis* (v. superior), an inferior which in the recent condition is concealed in part at this stage by the maxilla and is the *prominentia maxillaris* (v. inferior); an anterior which is perhaps the most striking of all, and is the forward continuation of the prominentia of the frontalis. This is the *prominentia anterior* (Pl. XI).

To the hinder aspect of the prominentia maxillaris the *musculus obliquus inferior oculi* is attached as usual.

The pars anterior is almost as long as the pars intermedia and the pars posterior taken together. It is deep behind where it is bounded by the sulcus antero-lateralis but gradually tapers in front and is smallest at the anterior extremity where it is slightly incurved to form a small cupula anterior, and a blunted cartilaginous process, the processus cupularis projects downwards from this cupular region. The inferior margin of this region is in great part incurved to form the *maxillo-turbinal*, but not far from its anterior end it is continuous with the outer edge of the lamina transversalis anterior, the site of continuity being bent upwards into the interior of the nose to form the *atrio-turbinal*, and in the concavity of this junctional region is found the *naso-lacrimal duct* (Pl. XI). No trace of a dorsal fenestra was found in the pars anterior.

Interior of the nasal capsule.

The lateral wall (Pl. XV).

This shows very beautifully the typical division into three segments, viz. the pars posterior (v. ethmoidalis), the pars intermedia (v. maxillo-atrio-turbinalis) and the pars anterior. Of these parts the pars posterior and the pars intermedia are of about equal size, though very different in form; the pars anterior, on the other hand, is greater in extent than the other two taken together. At this stage too the internal aspect of the lateral wall is exceedingly simple and bears out the statements of Voit, Seydel and Paulli.

The *pars posterior* appears as a roughly pentagonal concavity ending in the cupula posterior behind. It has the following boundaries, a posterior or postero-medial, an anterior (divisible into antero-superior and antero-inferior segments), a supero-lateral and an infero-medial.

The postero-medial border is short, lies in the sagittal plane, is placed in almost immediate contact with the septum nasi, but it is not anywhere fused therewith. It is so curved as to be concave forwards. The anterior border consists of two segments, one an antero-superior, the other an antero-inferior segment. These two meet in front at a very acute angle and form the free edges of the first ethmo-turbinal—a structure to be described later. The antero-superior segment of the anterior border commences above and behind at the anterior end of the supero-lateral boundary of the pars posterior, just where this part joins the pars intermedia. It passes forwards and downwards with

a somewhat wavy course to the acute angle above mentioned. The antero-inferior segment of this border springs from the anterior end of the infero-medial boundary of the pars posterior, runs forwards and upwards in a curve concave, downwards to reach and fuse with the antero-superior segment at the above mentioned acute angle. The two segments taken together form the anterior border of the pars posterior and at the same time the posterior boundary of the pars intermedia and the acute-angular region projects so far forwards as to reach into the pars anterior. The supero-medial border is free, concave upwards and medialwards. It stretches from the posterior boundary to the hinder end of the superior boundary of the pars intermedia, and forms the antero-inferior wall of the orbito-nasal fissure (Pl. X).

The infero-medial border is divisible into two segments, viz. the hinder which, rather less in length than the more anterior segment, is the median free edge of the lamina transversalis posterior. It comes into very close relation with the nasal septum but is nowhere fused with it. The remainder of this border is free and forms the hinder part of the lateral boundary of the fenestra basalis of the solum nasi (Pl. XI).

The medial surface of the pars posterior is concave and at this stage uninterrupted by the projection of any turbinals, the sole turbinal present being the first primary ethmo-turbinal in this region and that at the anterior limit of the pars posterior.

The *pars intermedia* is of large size and its long axis is placed at right angles to that of the pars posterior and pars anterior, and if the latter be looked upon as approximately horizontal the long axis of the pars intermedia may be regarded as vertical. It is completely shut off by the first primary ethmo-turbinal from the pars posterior, whereas it is for the upper half or so of its extent shut off from the pars anterior by the crista semicircularis. Below the crista semicircularis the pars intermedia is in direct continuity with the pars anterior. The pars anterior is so projected outwards as to cause enormous prominences on the paries nasi and these projections have already been described as the prominentia superior, prominentia anterior and prominentia inferior. Corresponding with these prominences on the exterior are hollows or recesses in the interior. These are a recessus superior or frontalis, a hollow which is bounded above by the superior margin of the pars intermedia, below and anteriorly by the anterior root of the first primary ethmo-turbinal, below and posteriorly by the freely projecting part of that turbinal. Anteriorly, the pars frontalis communicates directly with a very deep and anteriorly projected recess, the recessus anterior, whilst below it is continuous over the free edge of the anterior root of the first primary ethmo-turbinal with the recessus inferior (v. maxillaris). The floor of the recessus frontalis is practically uniformly concave, as it as yet has no frontal turbinals developed in it.

The recessus inferior v. maxillaris is very deep and largely hidden from medial view by the overhanging first primary ethmo-turbinal. It is in the recent condition almost completely occupied by the lateral nasal gland, whose

duct can be traced forwards almost to the front of the pars intermedia. Anteriorly and superiorly the recessus inferior (v. maxillaris) is continued without interruption into the recessus anterior which is of great depth. Inferiorly the recessus inferior is bounded by the incurved lower margin of the pars intermedia, whilst anteriorly the recessus inferior is directly continuous with the pars anterior below the level of the crista semicircularis. The *recessus anterior* is unusually large, and overhung from the front by a very deep crista semicircularis. It forms the prominentia anterior of the exterior, communicates supero-posteriorly with the recessus superior and infero-posteriorly directly with the recessus inferior.

From the posterior third of the superior margin of the pars intermedia the orbito-sphenoidal (nasal) commissure passes backwards.

The pars anterior of the medial aspect of the lateral wall is by far the largest segment of this aspect being as 6 : 5 to the length of the pars intermedia and pars posterior taken together. Posteriorly it is bounded in part by the crista semicircularis, but below this runs without line of demarcation into the pars intermedia, anteriorly it ends at the incisura narina, superiorly it is bounded by the tectum nasi anterius, whilst the inferior boundary is formed by the maxillo-turbinal in greater part, but near the front by the atrio-turbinal. The general outline of this region tends to the triangular the base being backwards and the apex at the incisura narina.

This region apart from its length is characterized by the presence of three turbinals, viz. the naso-turbinal, the maxillo-turbinal and the atrio-turbinal, but the two latter are confluent at this stage so that the term *maxillo-atrio-turbinal* is appropriate for the conjoined mass.

The naso-turbinal is very low in height, little more in fact than a slightly rounded elevation commencing behind at the crista semicircularis in its upper half, and running downwards and forwards for a short course to die away.

The maxillo-atrio-turbinal is of great length and the maxillary part specially so. It commences behind as the incurved lower margin of the pars intermedia and continues forwards as far as the hinder edge of the lamina transversalis anterior where it is confluent with the atrio-turbinal. It is so curved inwards and upwards that a well-marked gutter runs along its upper aspect in its whole expanse, the sulcus supra-conchalis. On its under aspect in the hinder half is the maxilla, whilst below it in its anterior half runs the naso-lacrimal duct. The atrio-turbinal segment of the maxillo-atrio-turbinal is practically caused by a folding of the floor of the anterior segment of the capsule over the underlying naso-lacrimal duct. This folding takes place along the line of junction of the lamina transversalis anterior with the under margin of the lateral wall of the nasal capsule. It is directly continued behind with the maxillo-turbinal, no incisura such as Voit describes in the rabbit being present at this stage.

In front of the maxillo-atrio-turbinal the inferior border of the lateral wall is also slightly incurved and at the same time curved upwards and medially.

It ends at an angular process which is formed by the junction of this border with the anterior border of the pars anterior.

The upper border of the pars anterior gradually slopes downwards from behind. It is formed by the tectum nasi anterius which is of very great thickness in its whole length.

Now a word or two may be said regarding the two great projections into the nasal cavity from the medial aspect of the lateral wall, viz. the first primary ethmo-turbinal and the crista semicircularis. These are of fundamental importance because they are the means of dividing the lateral wall into its three main divisions.

The first primary ethmo-turbinal is of great size and forms the boundary between the pars anterior and the pars intermedia and not only that but by its medial surface forms a considerable part of the lateral wall of the pars posterior, whilst its lateral surface forms the medial wall of the pars intermedia. It springs in the usual way from the lateral wall, viz. by three roots, the main root springs from the lateral wall along the curved line corresponding precisely with sulcus postero-lateralis on the exterior. This primary root is joined at right angles at its middle and on its lateral aspect by the anterior or third root (which in Tatusia is unusually large), forming a floor to the recessus frontalis and a roof to the recessus maxillaris. It passes forwards and upwards to end in the lateral wall of the recessus anterior.

After resolution from its three roots, the first primary ethmo-turbinal projects forwards and inwards and comes to an end in a pointed extremity which conceals from view part of the entry into the pars intermedia and even projects forwards far enough to reach the pars anterior.

The crista semicircularis, which partially separates the pars intermedia from the pars anterior commences at the upper portion of the pars intermedia and passes at first downwards and forwards, then downwards and backwards dying away gradually at its lower end. It forms the medial wall of the prominentia anterior and corresponds at its attached border with the sulcus antero-lateralis on the exterior. On the medial side of its upper end is found the inner end of the foramen epiphaniale.

Septum nasi (Pl. XV).

This is the forward continuation of the interorbito-nasal septum, is of great length, longer than the combined length of the pars trabecularis and pars chordalis, and though of considerable height, that height is altogether dwarfed by its great length. It consists of two parts, viz. a posterior which is subcerebral and an anterior which is precerebral. The two parts are of about equal length.

The subcerebral part projects freely above into the cavum cranii and as yet is unconnected laterally with any lamina cribrosa and at its hinder border is only connected with the cupula nasi posterior by connective tissue. The upper margin of this segment then plays the part of a crista galli. The lower margin

is much thicker than the upper one and is thicker behind than in front. It has appended to it on each side a narrow cylindrical posterior paraseptal cartilage, which seems to have chondrified independently of the lamina transversalis posterior (Pls. XI, XV). This cartilage is co-extensive with the length of the under border of the subcerebral part of the nasal septum and it ceases abruptly at the anterior limit of this part of the under border, a connective tissue bridge alone connecting it with the hinder end of the anterior paraseptal cartilage.

The precerebral segment of the septum has upper and lower and anterior borders. The upper border in its whole length is united with the lateral wall of the nasal capsule through the tectum nasi anterius and not far from its anterior end becomes greatly thickened, the thickening extending some distance from the septum. This thickening is the basis of a septo-turbinal.

The lower border is for the most part free and somewhat arched from behind forwards, anteriorly it is directly fused with the lamina transversalis anterior and through it connected with the lateral wall of the capsula nasi. Along the infero-lateral aspect of the free part of the under border lies the anterior paraseptal cartilage but this is separated from the septum itself by a narrow septo-paraseptal fissure.

The anterior border of the septum nasi is oblique and extends forwards and upwards from the anterior end of the lower border. At its lower hinder part it gives off on each side a small processus lateralis ventralis. There is no internarial foramen in the septum such as is met with in the rabbit (Voit), Microtus (Fawcett).

The solum nasi (Pl. XI) is relatively imperfect, though of great antero-posterior length. Posteriorly the solum nasi is represented by a lamina transversalis posterior which, considering the large size of the nasal capsule is extremely small; moveover, it is not so flat inferiorly as is usually the case. It is, however, pointed posteriorly. Anteriorly the lamina ends in a very oblique margin which is directed obliquely from within forwards and outwards and connected with its commencement by fibrous tissue is the posterior paraseptal cartilage. The medial edge of the lamina transversalis posterior is free of the septum nasi, being separated from it by a narrow fissure which is the backward continuation of the septo-paraseptal fissure. The anterior edge of the lamina transversalis posterior is the hinder boundary of the long fenestra basalis.

The lamina transversalis anterior, another constituent of the solum nasi, is of small size and at this stage perhaps more pro-cartilaginous than cartilaginous. It may be traced from the infero-lateral margin of the septum nasi in a downward direction at first separated only by a narrow fissure from its fellow of the opposite side. It then curves outwards, being convex downwards, next it bends suddenly upwards, vertically and rebends downwards over the underlying ductus naso-lacrimalis to form the atrio-turbinale after which it joins the lower margin of the lateral wall of the nasal capsule. The lamina transversalis anterior forms at once the anterior boundary of the fenestra

nasalis and the posterior boundary of the incisura narina. From the medial part of its hinder edge the anterior paraseptal cartilage is projected backwards.

The paraseptal cartilages (Pls. XI, XV).

These are anterior and posterior, and so far as I know they do not unite to form a common paraseptal cartilage.

The *anterior paraseptal cartilage* commences in front as a backward continuation of the median part of the hinder edge of the lamina transversalis anterior and is continued backward along the infero-lateral aspect of the lower border of the precerebral segment of the septum nasi in almost the whole extent of the latter. From its very commencement anteriorly it is in the form of a plate concave outwards and very soon the concavity lodges the organ of Jackson which is of great length. At the hindmost end of this organ the paraseptal cartilage becomes cylindrical and rod-like and soon comes to an end. By its lateral aspect the anterior paraseptal cartilage forms a considerable part of the medial wall of the fenestra basalis. Its medial aspect anteriorly is separated from that of its fellow by a narrow interval only, but further back and in fact for the remainder of its extent the gap between the two cartilages is considerable. From the septum nasi the anterior paraseptal cartilage is separated by a fissure—the septo-paraseptal fissure. On the infero-medial aspect of the anterior part of the anterior paraseptal cartilage is placed the independently ossified paraseptal process of the os incisivum; more will be said of this later.

The posterior paraseptal cartilage, not quite so long as the anterior is placed at the infero lateral aspect of the inferior margin of the subcerebral part of the septum nasi from which it is separated by a narrow septo-paraseptal fissure. It is a cylindrical rod-like structure, not continuous with the anterior paraseptal cartilage but separated by a small gap from it, medial to which lies the primordium of the vomer, which is not yet ossified. Posteriorly the posterior paraseptal cartilage reaches, but does not fuse with, the lamina transversalis posterior. This cartilage forms part of the medial boundary of the fenestra basalis.

The cartilaginous skeleton of the visceral arches (Pls. XII, XIII).

That of the first arch is represented from behind forwards by the incus, malleus and Meckel's cartilage.

The *incus* is of enormous size, consisting of a body, and two processes. The posterior process or processus brevis is very large and passes backwards from the body along the outer aspect of the pars canalicularis of the auditory capsule lying in a sulcus, the sulcus incudis, below the tegmen tympani and the prominentia semicircularis anterior. It is completely uncovered, so lies freely at the lateral aspect of the auditory capsule. The processus longus is very large, but perhaps actually shorter than the processus brevis; it descends from the corpus incudis, is facetted anteriorly and keyed in the usual way to the malleus

cartilage, but the connection between the two is by means of dense cellular tissue, for no joint cavity is as yet developed.

The *malleus* cartilage, placed directly in front of the incus cartilage, is like the latter, of enormous size. It consists of the usual parts. The manubrium is very thick antero-posteriorly and at its lower end bends sharply towards the pars cochlearis of the auditory capsule, and the musculus tensor tympani is attached to its medial side just above the bend above mentioned. The posterior surface of the body of the malleus cartilage is articulated to the incus in the way already mentioned. From the front of the body projects the third element in the first arch, viz. Meckel's cartilage.

Meckel's cartilage is here represented as a long cylindrical rod which runs a somewhat sinuous course forwards till it arrives opposite the lamina transversalis anterior of the nasal capsule, when it fuses with its fellow of the opposite side and comes to an end.

Traced forwards from the malleus cartilage it runs at first an arched course upwards and forwards, then it descends gradually for some distance, at the same time going somewhat medially. It then arches upwards, then downwards, again upwards slightly, and finally runs straight forwards to fuse with its fellow; during the whole of this sinuous course it is making inwards.

On the outer side of the anterior three-fourths or so the ossified mandible lies, but this does not quite reach forwards to the anterior extremity of the cartilage, so that a part of the lateral surface of the latter remains uncovered by bone.

No bone appears on its medial aspect, not even a geniale at its posterior end, though it may later, as there seems to be a collection of densely aggregated cells which suggest a goniale. The chorda tympani nerve runs through this mass and for some distance accompanies Meckel's cartilage forwards.

The cartilages of the *second* visceral or *hyoid arch* are the stapes, processus styloideus, and cerato hyal at this stage.

The stapes is of comparatively large size, perforated by a large opening through which a very small stapedial artery runs. Its foot rests against the cellular lateral wall of its vestibular cavity whereas its head articulates by dense cellular tissue with the inturned lower extremity of the processus longus of the incus cartilage. The musculus stapedius is inserted into the hinder lower aspect of its neck, and the main mass of the cartilage is separated from the anterior surface of the pars canalicularis by the nervus facialis. It has lost all connection with the processus styloideus.

The processus styloideus commences in a posterior hook-like piece (Pls. XII, XIII) which is bent down in front of the crista parotica but is still separate from the latter although connected to it by cellular tissue which is in process of chondrification. From the hook-like bend the processus styloideus descends almost vertically and parallel with the line of the manubrium mallei, then it suddenly bends forwards slightly upwards and slightly inwards and runs forwards and inwards to near the middle line where it comes to an end. At

right angles to this anterior extremity is placed the cerato-hyal which is connected to the processus styloideus by dense cellular tissue. The cerato-hyal lies with its long axis in the sagittal plane, supero-laterally it is connected with the anterior extremity of the processus styloideus whilst inferiorly it rests on the junctional region of the thyro-hyal and the basi branchial.

The cartilage of the third or thyroid arch is long, rod-like and almost cylindrical. It commences behind in a somewhat pointed extremity which rests upon a very small superior cornu of the corresponding ala of the thyroid cartilage. It runs forwards and inwards gradually increasing in thickness and near the middle line is jointed on to the side of the basi branchial. The basi branchial (body of hyoid) is somewhat wedge-shaped as seen from the front, the thin edge of the wedge being downwards, and the whole mass is wedged in between the anterior extremities of the thyro-hyals. As above said, on the junctional region of thyro-hyal with basi branchial, the cerato-hyal rests.

The cartilage of the *fourth* visceral arch, viz. the ala of the thyroid cartilage, is of considerable size. It is in the form of a quadrilateral plate curved from behind forwards and inwards towards the middle line, where it fuses with its fellow. At each of its posterior angles a small cornu is developed by which, in the case of the upper posterior angle, it articulates with the hind end of the thyro-hyal, and by means of the lower angle or cornu articulates with the cricoid cartilage. About its middle the ala is perforated by a foramen whose origin has been described in the account of the 12 mm. embryo. The symphyseal region of the two alae is the narrowest in vertical height of the parts of the thyroid cartilage. It is overlapped from above and in front by the basi branchial cartilage.

The cartilage of the *fifth* arch, viz. the cricoid, is well formed and for all practical purposes complete. On its summit are perched in the usual manner the arytenoid cartilages.

4. The Osseous Skeleton (Pls. XI, XIII).

Only covering or membrane bones are ossified at this stage, and being stained by Mallory's method are very easily located and modelled. The bones ossified at this stage are the os incisivum (paraseptal process only), the maxillare, palatinum, frontale, zygomaticum and mandibula.

The *os incisivum* is, as above said, only developed so far as its paraseptal process is concerned, and this lies on the infero-medial aspect of the anterior part of the anterior paraseptal cartilage a short distance behind the junction of the latter with the lamina transversalis anterior. Below the septum nasi and opposite the gap between the anterior and posterior paraseptal cartilages, a collection of densely aggregated cells is seen which I take to be the primordium of the vomer, but no trace of ossification is visible here at this stage.

The *os maxillare* is of great interest at this stage, and consists of two almost independent parts, the junction between them being by a very narrow bridge

of bone. The appearance is highly suggestive of double ossification, a condition I have never previously met with.

The two parts in question are a medial and a lateral.

The median part is an elongated mass of bone which lies on the under aspect of the maxillo-turbinal reaching from a point about opposite the middle of the anterior paraseptal cartilage in front to the lowest point of the maxillary prominence of the pars intermedia behind; cut coronally it shows three surfaces, viz. a lateral free or facial surface, a medial surface directed towards the nasal capsule and an inferior or buccal surface. Along the anterior third of its upper border the naso-lacrimal duct runs forwards. The lateral part is a leaf-like plate of bone separated for the most part by a wide gap from the median part but connected by a narrow stalk with the latter anteriorly. It conceals from lateral view the maxillary prominence of the pars intermedia of the nasal capsule.

The *ox zygomaticum* is placed some distance behind the lateral part of the maxillare and below the eyeball. It is a long splint-like bone which covers from the side the upper part of the hinder fourth of the mandibula, from which however it is separated by a considerable interval.

The *os palatinum* lies in its usual position, viz. below the lamina transversalis posterior. Seen from behind it is a somewhat triangular plate whose base is directed forwards, and whose median basal angle is likewise slightly projected somewhat forwards over the antero-median part of the lamina transversalis anterior. Its outer side is curved in a downward direction whilst its apex is directed backwards below the maxillary division of the fifth nerve.

The *os frontale* is an elongated plate-like bone which commences anteriorly at the hinder part of the prominentia frontalis of the pars intermedia of the nasal capsule, and is continued back over the lateral aspect of the sphenoethmoidal commissure and the basal region of the ala orbitalis, ceasing at a line drawn transversely through the optic foramen.

The *mandibula* is by far the largest of the bones ossified and forms a plate-like bone commencing in an anterior pointed extremity not far from the conjoined anterior extremities of Meckel's cartilages; it runs backwards on the lateral side of that cartilage as far back as or perhaps a little beyond the plane of the zygomaticum where it comes to an end in a pointed posterior extremity. Its upper margin deep to the zygomaticum rises to form a coronoid process into whose medial side the musculus temporalis is inserted.

The medial alveolar wall is developed as an upgrowth from the medial aspect of the main mass opposite the second fourth of Meckel's cartilage from the front. It commences as a plate-like offshoot of the main mass and insinuates itself between that and Meckel's cartilage, but further back it runs more like a splint along the lateral aspect of the cartilage. The anterior end of the main mass of the mandible is much fenestrated and through one of these fenestrae the mental nerve issues.

The vomer is not yet ossified, but its fibrous primordium can be seen

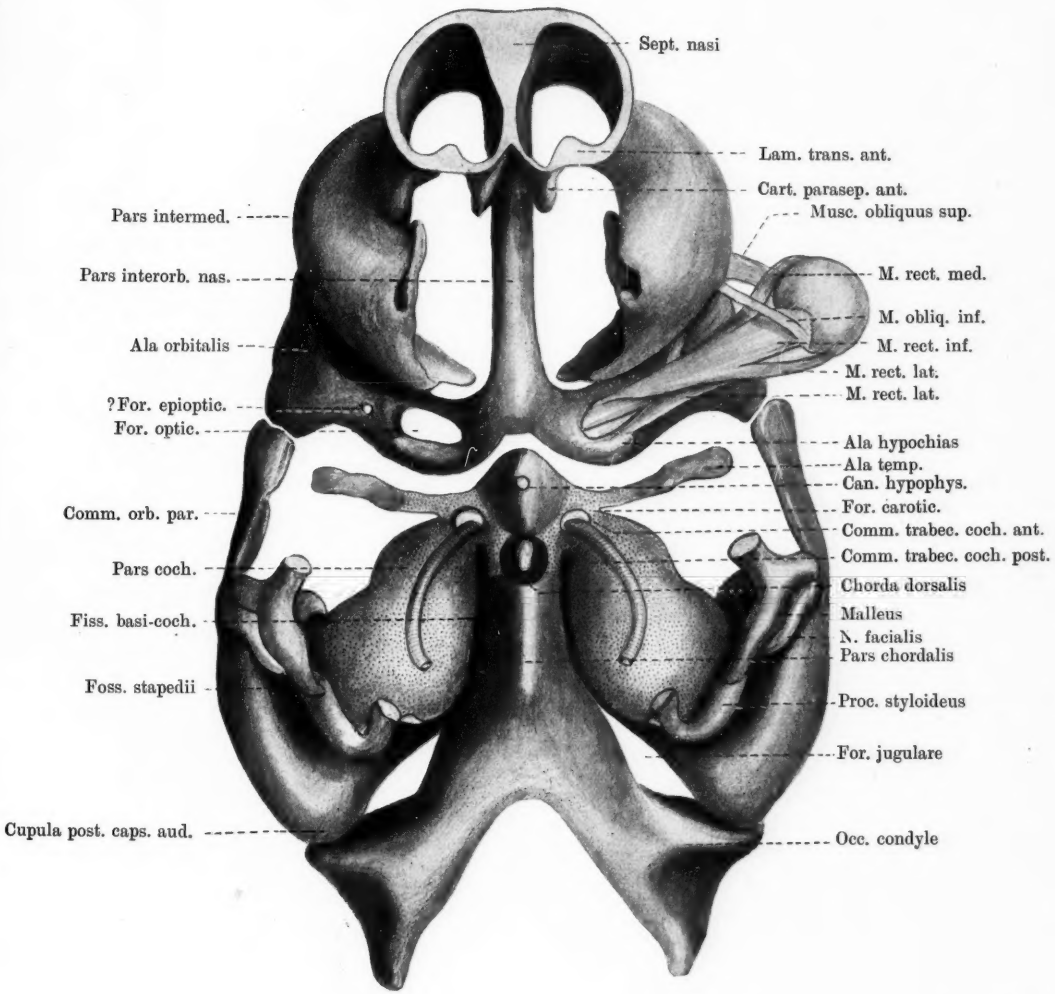
occupying the interval between the anterior and posterior paraseptal cartilages (Pl. XIV). Its position raises an interesting point in regard to this bone, a point which has already been dealt with in this Journal.

The models from which these descriptions are taken were made some five years ago, but publication has been delayed for many reasons. I had hoped to be able to obtain specimens of 25 mm. and 30 mm. total length, but have been unable to do so. Such specimens, I think, would have brought to light several obscure points. Details have already been described of the anterior end of the nasal capsule at the 60 mm. stage (os septo-maxillare in this Journal, vol. LIII. July, 1919).

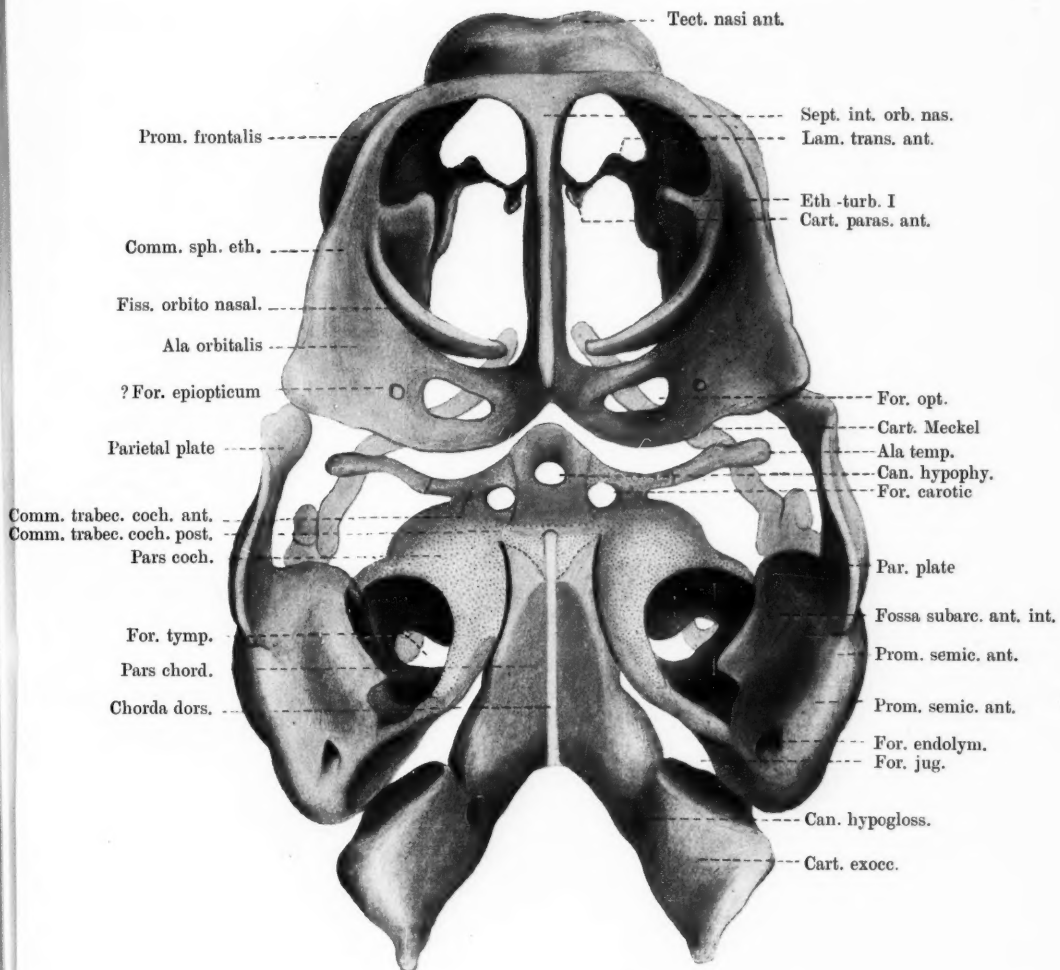
SUMMARY

The points of special interest which the models above described bring out are:

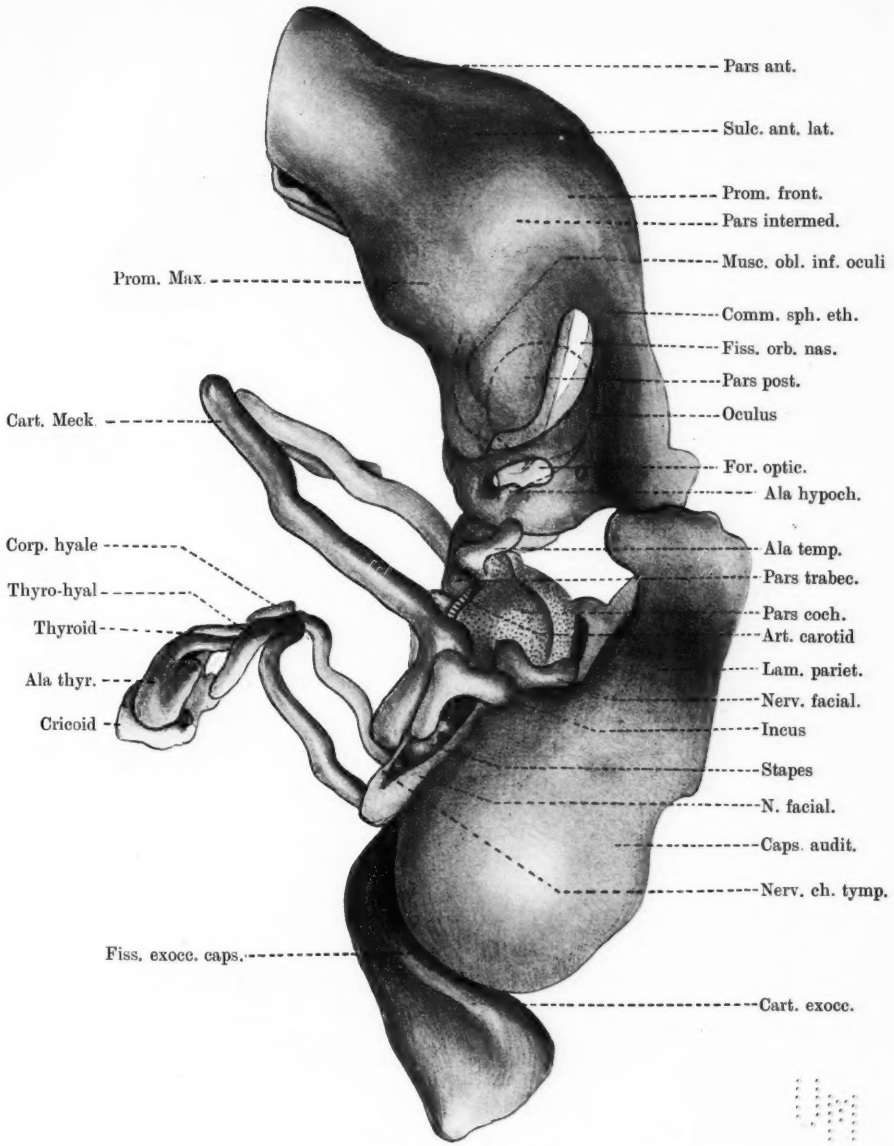
1. The formation of three independent masses of cartilage in the central stem, viz. the chordal plate, the trabecula, and the interorbito-nasal septum. I have not found double chondrification of the trabecula in these stages.
2. The large size of the incus and malleus cartilages.
3. The apparent independent chondrification of the posterior paraseptal cartilages, i.e. independent of the lamina transversalis posterior.
4. The late union of the parietal plate (lamina parietalis) with the ala orbitalis to form an orbito-parietal commissure.
5. The presence of a foramen (? epioptic) in the ala orbitalis lateral to the optic foramen.
6. The curious mode of union of the pre- and post-optic limbs of the ala orbitalis with the interorbito-nasal septum.
7. The independent chondrification of the ala hypochiasmata, and its subsequent fusion with the interorbito-nasal septum or with the post-optic limb of the ala orbitalis.
8. The mode of formation of a somewhat high type of ala of the thyroid cartilage from the simple form like that of the mole, 4th arch, and the foramen in connection therewith.
9. The curious bent condition of the anterior end of the chorda dorsalis, suggesting intershifting of the pars chordalis and the trabecular part of the central stem.
10. The independent ossification of the paraseptal process (Broom's "Prevomer") of the incisivum.
11. The probable double ossification of the maxilla.



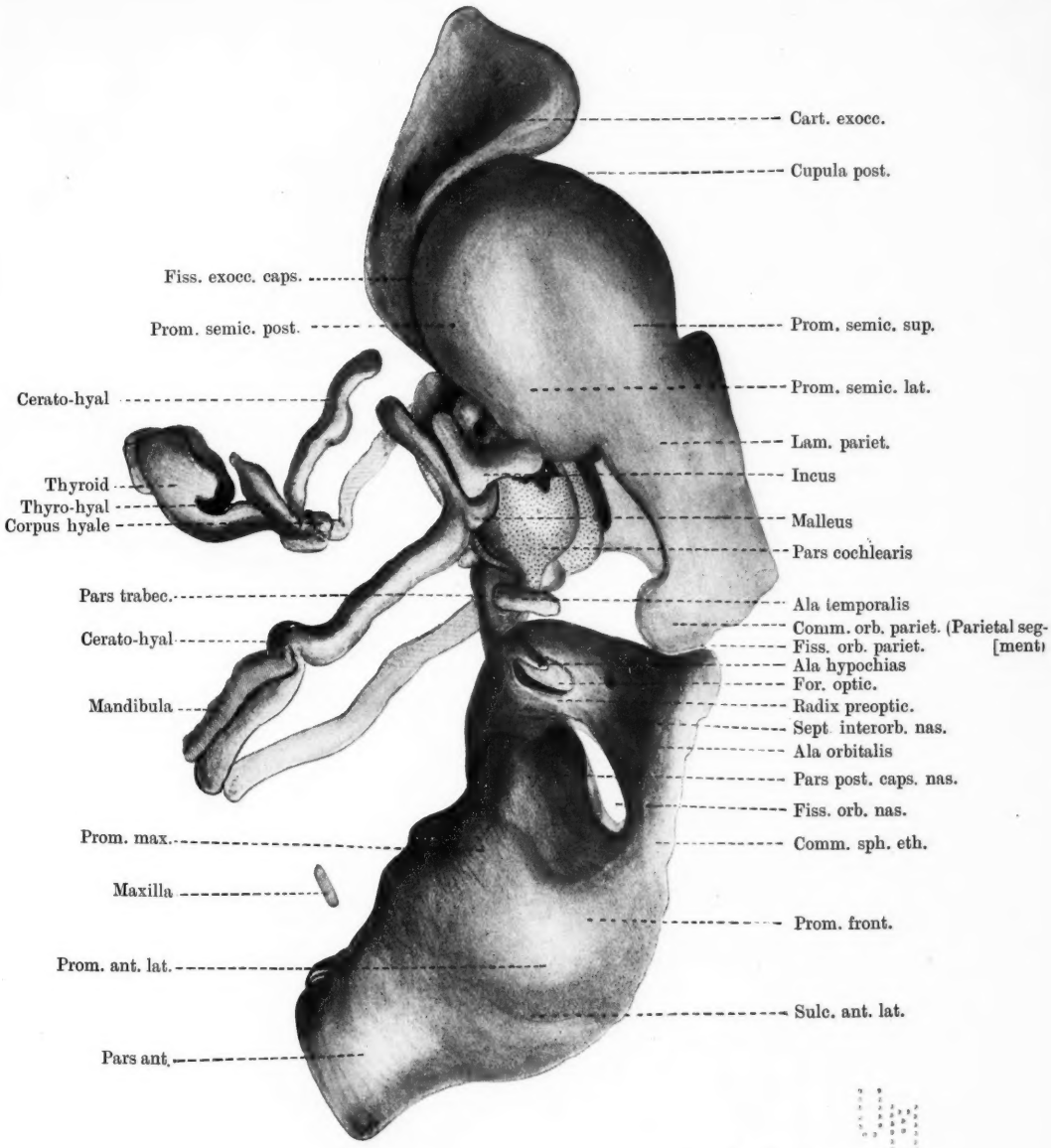
Tatusia Novemcincta. Chondrocranium of 12 mm. (Wood-Jones) embryo, from below. The parts dotted are unchondrified, the lamina transversalis anterior and the anterior paraseptal cartilages are procartilaginous.



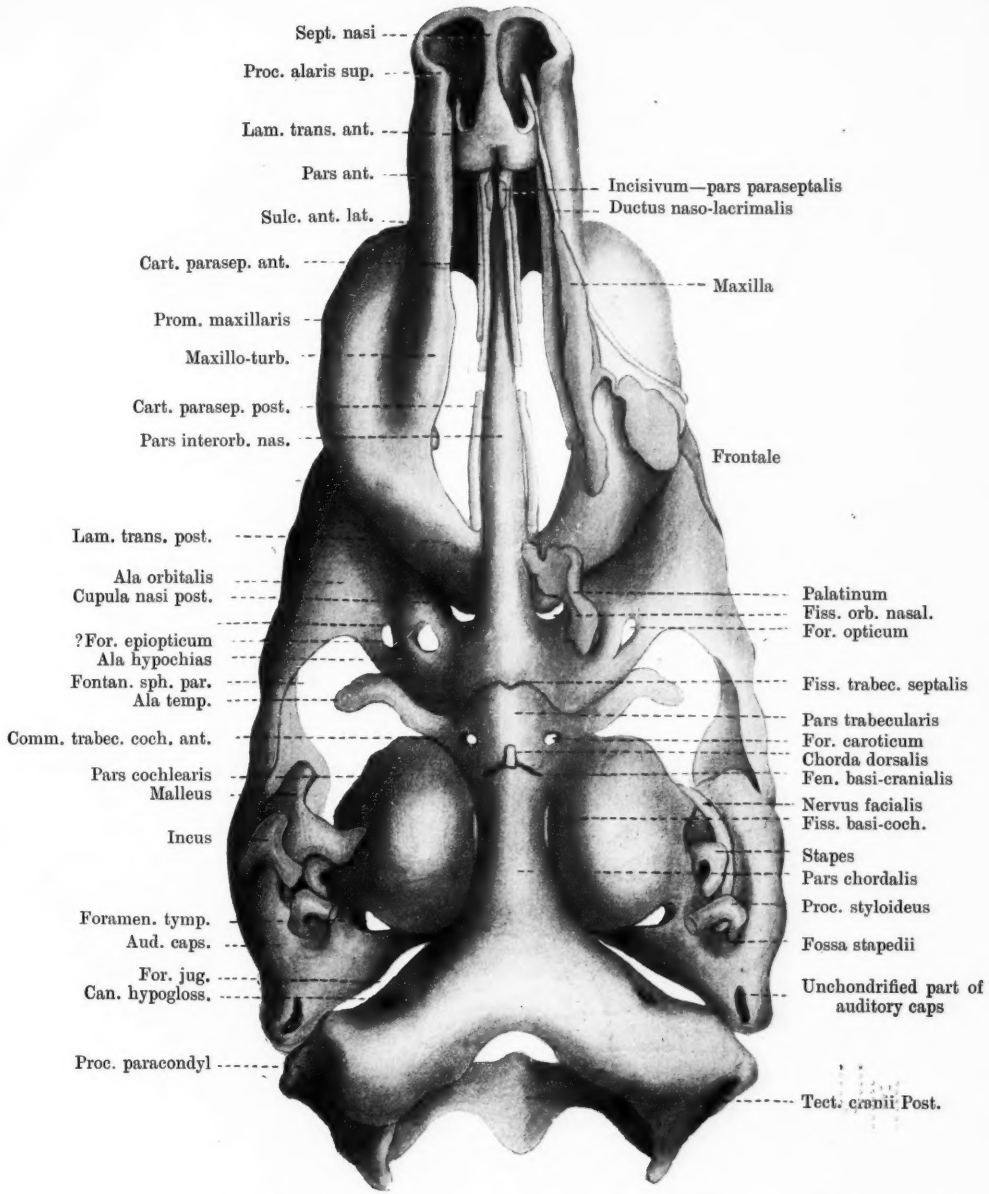
Tatusia novemcincta. Chondrocranium of 12 mm. (Wood-Jones) embryo, from above. Lamina transversalis anterior and anterior paraseptal cartilages are procartilaginous. All areas dotted are as yet unchondrified.



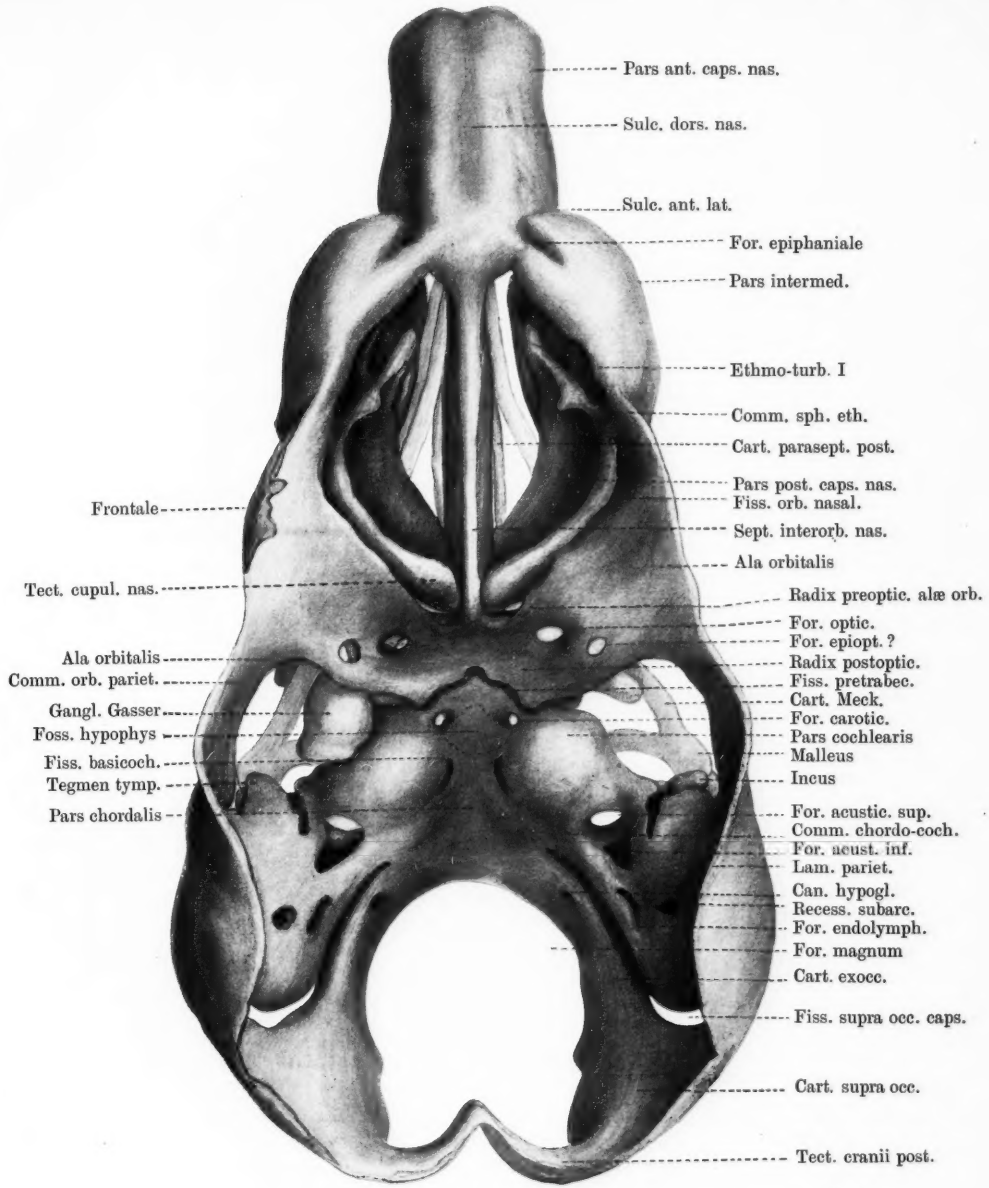
Tatusia Novemcincta. 12 mm. (Wood-Jones) embryo. Chondrocranium from left side.



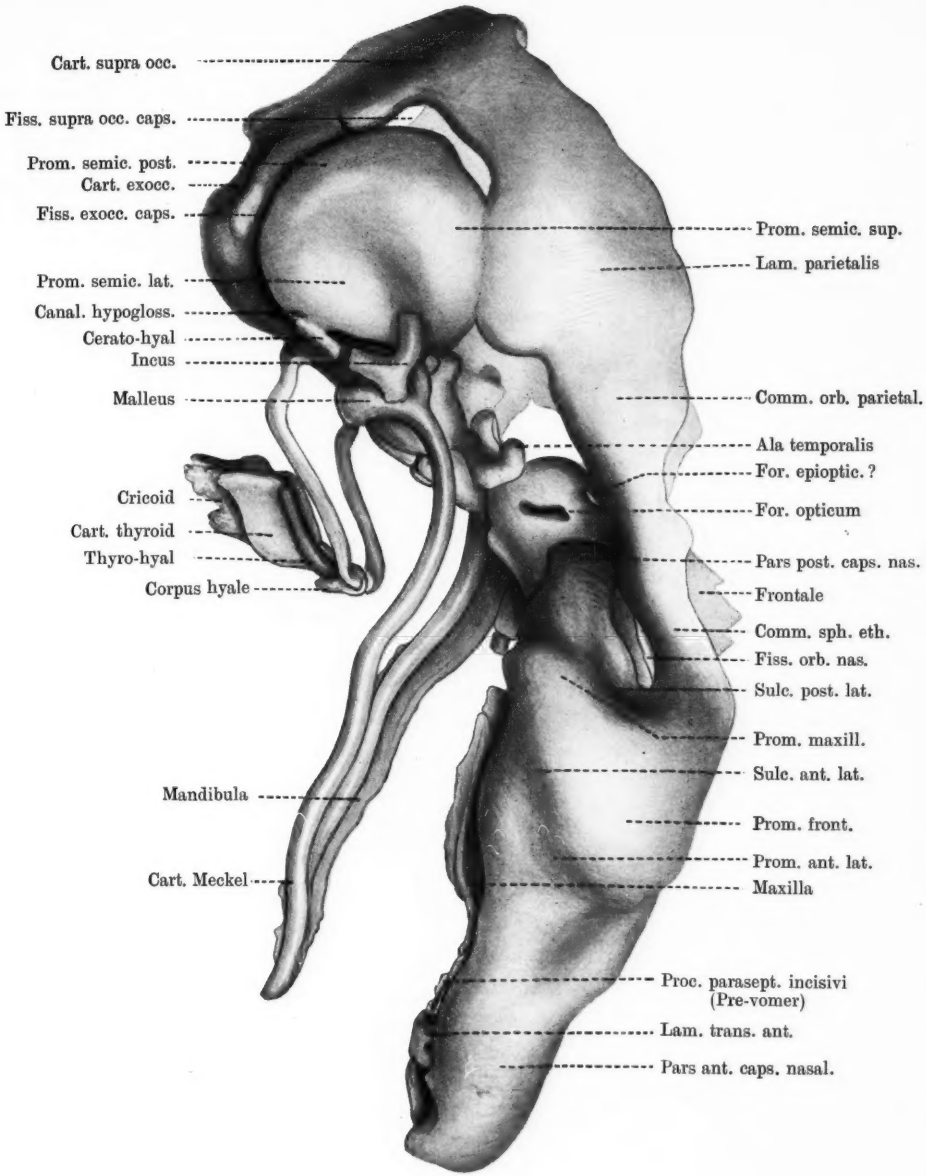
Tatusia Novemcincta. 12 mm. (Wood-Jones) embryo from right side. Unchondrified parts are dotted.



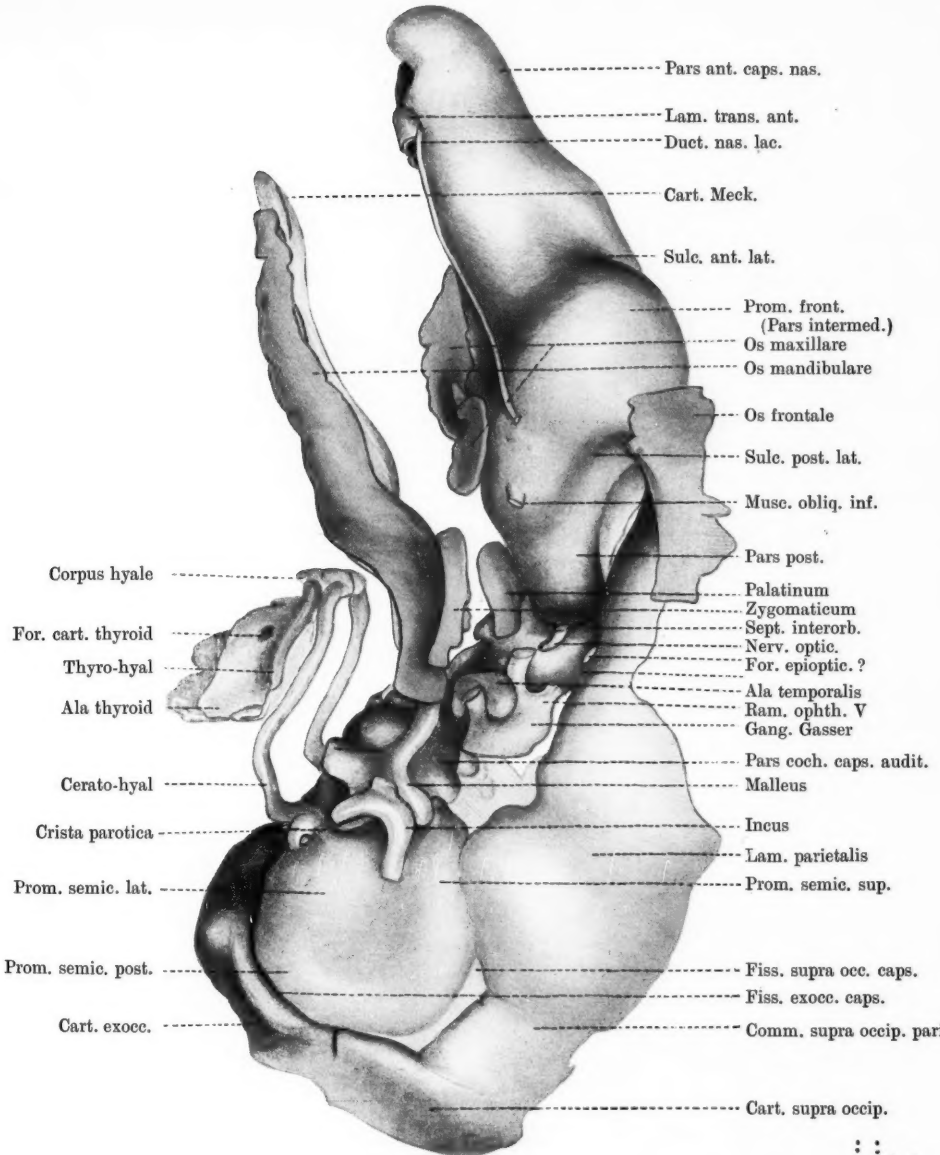
Tatusia novemcincta. Chondrocranium of 17 mm. (Wood-Jones) embryo, from below. The lamina transversalis anterior is unchondrified.



Tatusia novemcincta. 17 mm. (Wood-Jones) embryo. Chrondrocranium from above.



Tatusia novemcincta. 17 mm. (Wood-Jones) embryo. Chrondrocranium from right side.



Tatusia novemcincta. Chondrocranium of 17 mm. (Wood-Jones) embryo, from left side.

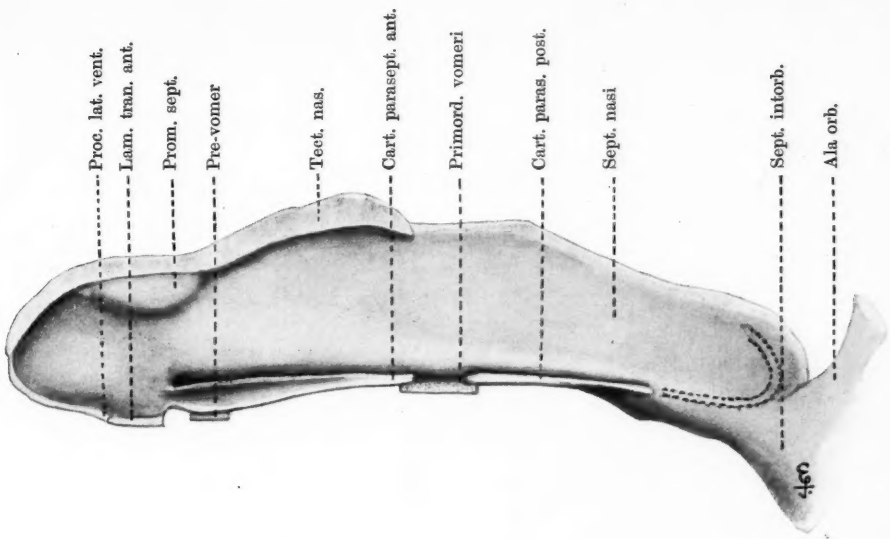


Plate XIV. *Tatusia novemcincta.* 17 mm. Septum nasi and appendages seen from left side.

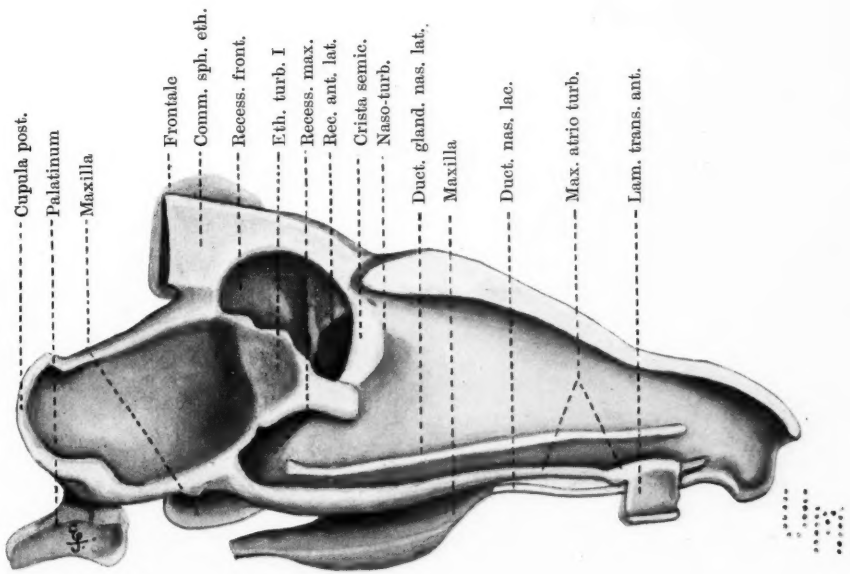


Plate XV. *Tatusia novemcincta.* 17 mm. Left wall of nasal capsule from within.